INTERMEDIATE BIOLOGY

BY THE SAME AUTHOR

Essentials of Biology (Heinemann)
Exercises in Biology to 'O' Level (Heinemann)
Maintenance and Production (Centaur Books)

A bat coming to land. (By courtesy of Prof. Harold E. Edgerton.)

INTERMEDIATE BIOLOGY

by

W. F. WHEELER, M.A.
Second Master, Royal Grammar School, Worcester

5755

Sixth Edition

HEINEMANN EDUCATIONAL
BOOKS LTD · LONDON

Heinemann Educational Books Ltd
LONDON MELBOURNE TORONTO
SINGAPORE CAPE TOWN
AUCKLAND IBADAN
HONG KONG

Original Illustrations by
M. W. MAUD JEPSON, M.Sc.
W. E. S. POWERS, B.Sc., A.R.C.Sc.
C. G. GARDENER, M.A.,
and T. A. G. WELLS, B.Sc., Ph.D.

Sixth Edition © W. F. Wheeler 1962

First published 1940
Reprinted 1941
Second Edition, 1942
Reprinted 1943, 1944, 1945
Third Edition, 1947
Reprinted 1947, 1948
Fourth Edition, 1952
Reprinted 1953, 1954
Fifth Edition 1956
Reprinted with alterations 1958
Reprinted 1959
Sixth Edition revised throughout 1962
Reprinted 1962
Reprinted with alterations 1963
Reprinted with alterations 1965

570
W561g

Published by
Heinemann Educational Books Ltd
48 Charles Street, London W.1
Printed in Great Britain by
Bookprint Limited, Kingswood, Surrey

Foreword

by Professor Eric Lucas

The growth of the sciences which describe living matter has been so rapid since the beginning of this century, that it now requires courage to write a text-book, even for School use, bearing on its cover the title 'Biology'. The great increase, however, during the past twenty years, in the number of candidates at Ordinary Level presenting this subject, shows that its importance is being increasingly realised. As an Advanced Level science, also, it has much to recommend it. By treating biology as a single subject the candidate is enabled to pursue both physics and chemistry to this standard, thus strengthening the scientific training of the future biologist. As a part of a general education, whether of future medical students or others, the claims of the science of life must be stronger than those of any other science. It is therefore surprising that although several good text-books of botany and zoology are available, the needs of the parent science have been largely neglected, except at a very elementary stage. This tendency to separate biology into its daughter sciences is, in my view, unfortunate. It may possibly make the subject matter more straightforward for some students, and perhaps the organisation of the work becomes simpler, but the danger of overlooking the similarities between the groups of living organisms and the general principles which apply to all is, in my experience, very real.

The apparent lack of co-ordination between University botany and zoology departments and the unwillingness of some authorities to set Biology papers in their Scholarship examinations have already influenced unduly the biology courses in schools. In advanced work this departmentalism is unavoidable, but it would be a pity if the study of the wider subject were, on this account, to be discouraged in the earlier stages.

As a school subject biology is still in its infancy, and methods of teaching it must all be regarded as in the experimental stage. Some of his readers will no doubt differ from Mr Wheeler as to the scope of his book, and details of treatment, but all should applaud his successful effort to unite the various sub-sciences into an organic whole. The result of his work is no mere combination of elementary botany and zoology, but a synthesis which brings out clearly the principles of biology, and the inductive methods so characteristic of this science. By selecting material wisely and avoiding irrelevant issues, the author shows clearly the main lines on which the science has developed. The early sections of

his book provide a sound foundation of morphology and anatomy, thus automatically retracing the historical development of the science. He is not content, however, to dwell too long on the comparative anatomy of the late nineteenth century, but uses his examples skilfully to introduce more recent developments. Comparative physiology and biochemistry, heredity, cytology and ecology all have their places, and there is a pleasing freshness of treatment which makes this up-to-date biology text-book very readable. Those who have read *Inheritance and Evolution* by the same author will expect to find these subjects competently elucidated, and will not be disappointed.

Besides being very suitable for forms taking biology at the Advanced Level, this book would serve admirably as a text-book for most Sixth form biology courses, whether the subject is the basis of a general scientific education or intended primarily for medical students. Where its subject-matter extends beyond these examination syllabuses, it is always stimulating and never directed towards premature specialisation. One might have wished for more information on the organism in relation to its environment, and possibly behaviour is a subject that could be more exploited, but this would be to ask the author to go too far ahead of the syllabuses.

It is to be hoped that more text-books of this kind will appear, for Mr Wheeler would be the first to admit that biology courses will need constant criticism and revision, as the subject grows, and as we improve our teaching methods. I am very pleased to be associated, in a minor way, with the production of this well balanced account of living organisms, for I feel that it represents another step forward in the teaching of biology in schools. I hope that it may commend itself to other teachers of this subject, for it seems to me to indicate the line along which biology may most profitably develop in Sixth forms.

Preface

This book aims at fulfilling the requirements of students for the Advanced and Scholarship Levels of the General Certificate of Education, and for First M.B. and allied examinations. Accordingly its contents are very largely predetermined. But its method of treatment is designed, so far as possible, to resist that tendency to the separation of the subject into two component halves, which divorces the study of the structure and function of animal organisms on the one hand from that of parallel phenomena in plants on the other. This present state of affairs may very well be due, at least in part, to the fact that the vast majority of text-books at this standard are concerned exclusively with zoology or botany, and only rarely in either is there any digression into the province of the other. This cannot but create a false impression in the mind of the student in respect of the true unity existing in the realm of living organisms, considered as a collective whole; the essential relationships between animals and plants are in consequence obscured. The ultimate object of a course in biology should be the recognition and description of the fundamental attributes, formal and functional, of living organisms, with the discovery of their essential uniformity, frequently masked by superficial diversity. Nor can this diversity be ignored. Only by a study of particular cases can general conclusions be reached.

Accordingly, Parts I and II of this book concern themselves with the description of the morphology of animal and plant types respectively. Subsequently animals and plants are considered comparatively in respect of their cellular structure, physiology, development, inheritance, evolution and relation to environment, in the hope that assistance may thus be provided to the student in the formulation of a true conception of the world of living things. This more comprehensive treatment of biology in schools may perhaps eventually be attained if only our universities will introduce Schools of Biology, as alternatives to the present specialised courses in zoology and botany, which are themselves responsible for supplying to teachers an unnatural bias right at the outset of their professional careers. A teacher of physics has taken his degree in that subject, and not merely, for example, in magnetism and electricity. It seems an unwarrantable injustice that the same opportunity should not be presented to intending teachers of biology.

I wish to record my most grateful appreciation to Professor Eric Lucas for the invaluable assistance he has rendered in the reading of the whole of my manuscript, offering constructive criticisms and suggestions on very many points. I am sensible of the honour which he has done me in

associating himself with this book to the extent of so kindly writing a foreword.

Miss Maud Jepson, M.Sc., has been responsible for some hundred illustrations, all of which bear her initials. Comments on her contribution are superfluous: the value of the work she did is at once apparent in the figures themselves. More than forty of the remaining original figures, mostly of apparatus, have been drawn by Mr H. A. Bennett, to whom my thanks are further due for the completion of the lettering of all the illustrations.

I wish also to thank the various authors and publishers who have kindly granted me permission to reproduce figures from their books. In each case a separate acknowledgment is made beneath the illustration taken. To Mr E. B. Ford and Messrs John Murray I wish to express my thanks for permission to copy figures of the mouth-parts of the cockroach from the *School Science Review*, Vol. XX, No. 80, pages 571–574.

For generous assistance in the matter of the morphogeny of floral organs I am indebted to Dr H. R. X. D'Aeth, of Gresham's School, Holt, whilst valuable criticisms were forthcoming from Mr Cyril Bibby, Mr E. Yerbury, of Liverpool Collegiate School, and Dr E. W. Shann, of Rugby School.

PREFACE TO THE SIXTH EDITION

In preparing the sixth edition advantage has been taken of the opportunity provided by resetting to introduce extensive revision of several important topics. For the benefit of those already familiar with this book a list of the major amendments is provided below. In earlier impressions many botanical topics have been revised in the light of extending knowledge; at the present juncture most of the new material involves more comprehensive and modern treatment of the various aspects of animal biology. At the same time resetting has made it possible to re-establish more of an organic unity for the book as a whole than is possible when changes are made piece-meal, largely circumscribed by existing pagination.

A number of illustrations have been substituted and for the new ones I am greatly indebted to Dr T.A.G. Wells, of the College of Technology, Kingston-upon-Hull, and to Mr C. G. Gardener, of the College of Advanced Technology, Birmingham. Mr Gardener has also very kindly supplied detailed criticisms of the zoology content of the book, whilst Dr L. W. Poel, of the Botany Department of the University of Birmingham, has rendered similar invaluable service in respect of the botany. To these gentlemen I offer my humble thanks.

In addition to many minor changes, the following are the more important of the major modifications.

(1) Parasitic Protozoa (page 13).
(2) Histology and physiology of *Hydra* (pages 25–32).
(3) Vascular and nervous systems of *Lumbricus* (pages 56 and 60).
(4) The insect cuticle (page 68).
(5) The tracheal system of insects (page 75).
(6) The mammalian organs of smell (page 173).
(7) Mammalian tissue histology (pages 324–349).
(8) Functions of liver (page 343) and of blood (page 354).
(9) The role of *DNA* (page 578).
(10) Extensive revision of the embryological section (pages 499–549).
(11) Polyploidy and multiple allelomorphism (pages 585–587).
(12) Mechanism of evolution and associated topics (pages 616–624).

I am indeed grateful to all those who have helped in this task of revision and to none more than to Alan Hill, managing director of my publishers, and in the later stages to his assistant, Hamish MacGibbon. Their skill and encouragement have done so much to solve my many problems.

Worcester, 1962. W.F.W.

In addition to a few minor corrections, the following topics have been revised or expanded in the current reprint:

(i) The action of the heart of the frog (page 126).
(ii) Mineral salts as food of higher plants (page 375).
(iii) Mammalian respiration (page 423).
(iv) Plant hormones, including kinins and phytochrome (page 495).
(v) Reproduction in *Euglena* (page 644).

Worcester, 1963. W.F.W.

The principal feature of the current reprint is the inclusion of a brief description of the biology of the rat (page 677), with reference to those features in which it differs from that of the rabbit. This has been done to meet the present-day requirements of several examining boards. Other relatively minor modifications concern:

(i) The boundary wall of bacterial cells (page 211).
(ii) The egg cortex and determination (page 516).
(iii) The significance of *RNA* and *DNA* (page 578).

Worcester, 1965. W.F.W.

Contents

Foreword *by Professor Eric Lucas* v
Preface vii
List of plates xii
Introduction xiii

PART I. ANIMAL ANATOMY

1 Amoeba and Paramecium. Parasitic Protozoa 3
2 Hydra and Obelia 25
3 Fasciola and Taenia 39
4 Lumbricus 52
5 Periplaneta 67
6 Scyliorhinus 81
7 Rana Temporaria 110
8 Oryctolagus 139

PART II. PLANT ANATOMY

9 Selected Algae 181
10 Fucus 192
11 Selected Fungi. Bacteria 200
12 Pellia. Funaria. Dryopteris 216
13 Pinus 230
14 Angiospermae. The Stem 238
15 The Leaf 253
16 The Flower 264
17 The Root 288

PART III. CELLULAR STRUCTURE OF ORGANISMS

18 The Cell and its Contents 301
19 Multiplication of Cells 310
20 Tissue Elements of Higher Animals and Plants 321
21 Division of Labour in Animals and Plants 352

PART IV. COMPARATIVE PHYSIOLOGY

22	Nutrition	369
23	Nutrition (*continued*)	389
24	Growth and Respiration	417
25	Elimination of Waste Matter	441
26	Irritability and Movement	453
27	Hormones	479

PART V. DEVELOPMENT AND REPRODUCTION

28	Embryology of Branchiostoma	499
29	Embryology of Rana	508
30	Embryology of Gallus and Oryctolagus	526
31	Germination	550
32	Life-Histories of Animals and Plants	556

PART VI. HEREDITY AND EVOLUTION

33	The Mechanism of Inheritance	569
34	Evidence for Evolution	591
35	Evolution of the Vertebrate Vascular and Urino-Genital Systems	607
36	The Mechanism of Evolution	616
37	Classification	626

PART VII. THE ORGANISM AND ITS ENVIRONMENT

38	The Inanimate Environment	639
39	The Animate Environment	663
	Appendix I	675
	Appendix II—The Rat	677
	Index	681

List of Plates

A bat coming in to land	*Frontispiece*
	Facing page
Early stages in leaf development	206
Resting nucleus of a salivary gland cell	207
Virus of tobacco necrosis	207
Streptococcus viridans	207
Section of a chloroplast of *Aspidistra*	238
Pit membrane in the radicle of maize	238
Photomicrographs of heads of mammalian spermatozoa	239
Scyphistoma of *Aurelia aurita*	239
Tubularia larynx	494
Anemonia sulcata	494
Young worker larvae in cells	495
Tadpole, showing the operculum	495
The birth of a mosquito	495
Proteus vulgaris	526
Blowfly eggs on teeth of rabbit	526
Head of mammalian embryo in the region of the fore-brain	527
Transverse section of mammalian oesophagus	527
Transverse section of testis of *Hydra*	527
Hydra, showing testes and attached embryo	527

Introduction

BIOLOGY – the science of life – is concerned with the properties, both formal and functional, of bodies which display in various conditions the characteristics from which the existence of life is inferred. Life itself is an abstract: its presence can only be deduced from its various manifestations in what are consequently called living organisms. These are customarily sharply divided into two groups – animals and plants. But before proceeding to a detailed description of living organisms it will be well to inquire into the fundamental features by which a living organism can be distinguished from a non-living body, and hence the properties by which protoplasm (living matter) is characterised.

Composition

A living body is largely composed of a vast number of highly complex chemical compounds, collectively constituting what is known as **protoplasm**. Very many of them cannot be analysed, since any attempt to do so results in the destruction of the protoplasm, through changes certainly in the physical, and probably also in the chemical, nature of its constituents. In accordance with the almost incessant activity of the living organism the protoplasm itself is undergoing continuous change, whether as a result of the formation of new material, or by destruction of some already present to bring about the release of the potential energy of the complex molecules to provide the kinetic energy necessary for work. With non-living substances the position is quite different. The great majority of them are stable and susceptible of analysis. Others are, of course, unstable, and may even be explosive. But even then they are capable of independent existence, whereas protoplasm is a complex mixture of substances. In physical nature, too, there is a sharp discrepancy between living and non-living matter. Thus non-living matter may exist as a solid, liquid or gas, whilst mixtures of the solid and liquid phase may represent any state from a mere suspension to a true solution. Protoplasm, in accordance with the complexity of the molecules of the chemical compounds which comprise it and with its very high percentage of water, acting as a continuous phase, occurs always in colloidal form. Since a study of protoplasm cannot be undertaken apart from the living organisms whose bodies it so largely comprises, the properties of this substance must be sought through a consideration of the form and functions of animals and plants themselves. The physical properties of protoplasm as a complex colloid are further described on page 307.

Increase in Bulk

Non-living matter can increase in bulk only as a result of the addition of identical material. Thus the growth of a crystal of copper sulphate can be achieved only by its suspension in a solution always saturated with that particular salt. Further, the addition of new material occurs only on the outside. But protoplasm increases in bulk by absorption and assimilation of material tolerably different from its own chemical compounds. Thus a horse may be fed on oats, and from the substances provided by this food it is capable of building up its own protoplasm. This discrepancy between the food absorbed and the protoplasm synthesised is even more marked in green plants. Thus the whole of the body, including the skeletal architecture as well as the protoplasm, is built up from water, mineral salts and carbon dioxide.

Movement

One of the chief characteristics of the vast majority of animals and of a few lower plants is the power to effect movement. Non-living bodies – e.g. a car – may also move. But it is quite apparent that the two are fundamentally dissimilar. One is a man-made mechanism, constructed so that the energy liberated as a result of the combustion of a mixture of petrol vapour and air may be utilised ultimately in the propulsion of the wheels of the vehicle. But in the living organism the movement is spontaneous. The two are alike in that each requires energy, obtained in the latter case through respiration, whilst just as the car is set in motion by human device, so some external, or perhaps internal, stimulus is necessary to initiate locomotion in a living organism. Another point of contrast lies in the fact that a car must be refuelled by an external agent, whereas a living organism replaces its own respiratory substances from the food which it absorbs.

Respiration

Respiration is the process in living organisms whereby energy is liberated for the performance of work. It takes place continuously and spontaneously, whilst its execution almost always involves the presence of atmospheric oxygen, though there are exceptions to this. Its occurrence in animals may often be detected by external movement, such as the raising and lowering of the hyoid apparatus in the throat region of the frog, and by the expansion and contraction of the thorax in mammals, as well as by the exhalation of water vapour and carbon dioxide. Respiration may be compared with combustion in machines, again noting the obvious differences, principal amongst which is the fact that in the latter the whole is initiated and controlled by human agency. Both result in the liberation of energy.

Irritability

All living organisms possess to various degrees the power to respond to external influences, or stimuli. This is evident both in animals and plants. Thus a plant illuminated from one side only will grow in the direction of the light, whilst a tendril, on making contact with any form of support, will climb round it. A consideration of our own everyday experiences will make it apparent that our almost every movement is regulated by external conditions. Non-living substances may well be affected by external conditions, though the response is obviously different. Thus a photographic plate is affected by light, whilst cold weather may modify the starting and running powers of a car, since the petrol will not readily vaporise at low temperatures. But however close may be drawn the analogy between the conduct of living organisms and non-living bodies in their response to external conditions, there remains this difference. Living organisms are better adapted to their environment through their powers of response, which always tend towards the preservation of them and their kind. Manifestly this cannot apply to non-living bodies.

Thus, so far as movement, respiration and irritability are concerned, it is evident that the analogy between living organisms and non-living bodies depends on the construction by man of machines which function on principles similar to those responsible for the performance of some of his own essential life-process, whether he did this consciously or unconsciously.

Reproduction

The powers of reproduction are the sole province of living organisms. In fact, the ability to reproduce may be described as a fundamental property of protoplasm, and so far as our experience goes, it can be formed in no other way. Thus *Amoeba*, for example, consisting of a minute speck of protoplasm crawling on the mud at the bottom of ponds, does not grow to an unlimited size, but on reaching a certain maximum divides into two, each of the products then increasing to adult dimensions before repeating the process. This simple type of reproduction is confined to the lower animals and plants, but in all the power to reproduce is present, though exercised less frequently and involving more complicated mechanisms. It should be noted, however, that certain of the viruses, of molecular size, present some difficulty. They reproduce like living organisms, but on the other hand they appear to exhibit some properties of non-living matter (see page 213).

PART I

Animal Anatomy

In this section a number of selected animal types will be described, and throughout it is the anatomy – *i.e.* the gross structure of the organism as a whole – which will be emphasised. But it is neither practicable nor desirable to divorce anatomy from the performance of essential life-processes, though the principal consideration of these latter will be reserved for Part III. In the simpler types, therefore, where the structural features are severely limited in extent, they will be related to their respective functions, whilst the treatment of forms which have attained to a higher degree of evolutionary development will be in the main descriptive of their anatomy only.

CHAPTER I

Amoeba and Paramecium
Parasitic Protozoa

I. AMOEBA

Amoeba proteus belongs to the group of animals known as the Protozoa. Members of this phylum differ from all other animals (Metazoa) in that they are non-cellular – *i.e.* their bodies are not divided up into cells. In the life of a single individual four stages can be recognised. They are the infant, which emerges from a spore (see page 8), adolescent, adult and senile stages, the last-named being recognisable by its failure to continue fission (see page 8). The structure described is of a typical adult.

Structure

Amoeba is a minute organism, of jelly-like consistency. It occurs on the mud at the bottom of fresh-water ponds. Its entire body is composed of **protoplasm** (living matter). This is clearly differentiated into a comparatively clear, peripheral **ectoplasm**, surrounding a more granular **endoplasm**. Within this latter are contained several structures of importance. The **nucleus** may be distinguished as an oval body, slightly more opaque than the remainder of the endoplasm. It controls the metabolic activities (page 369) of the organism. Scattered throughout the endoplasm is a number of granules, consisting principally of minute ciliates or Algae, in various stages of digestion and which the animal uses

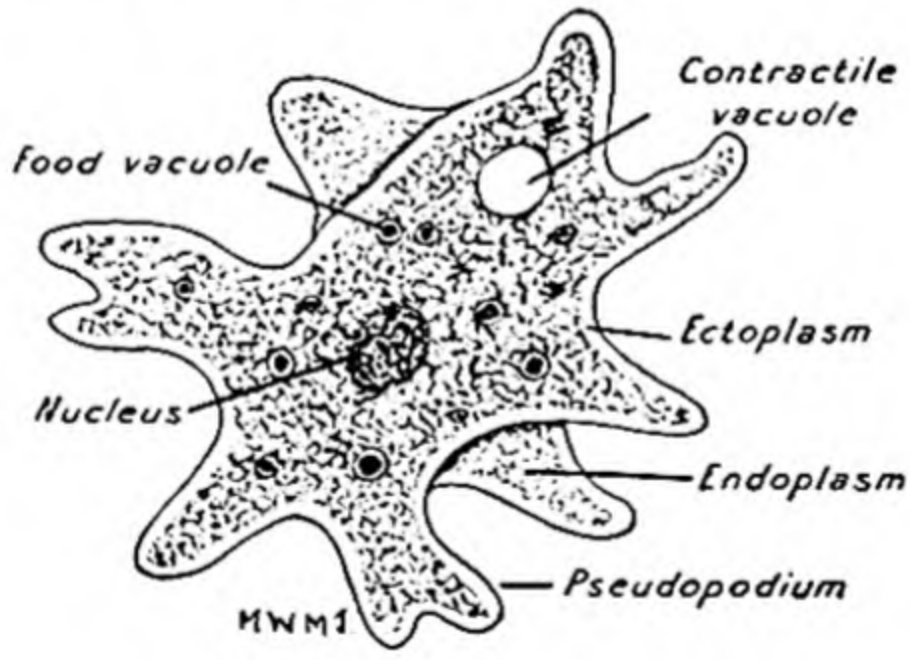


FIG. 1 – *Amoeba proteus.*

as food. Each is enclosed within a drop of fluid, the whole constituting a **food vacuole**. A clear region, spherical in shape, may frequently be identified in the endoplasm. This is the **contractile vacuole**. The whole body is of incessantly-changing shape, each major projection being termed a **pseudopodium**. It has recently been established that a certain degree of polarity exists in *Amoeba*, the posterior end being distinguishable by the somewhat wrinkled appearance of the ectoplasm. The significance of the various structures, to which the term '*organelles*' may be applied, thus distinguishing them from the true organs (page 359) of higher forms, may best be understood by a study of the way in which they accommodate the performance of the essential life-processes of the animal.

Pseudopodia

Pseudopodia are associated with several important functions. Though the volume of a single amoeba remains constant (apart from the slow and continuous process of growth), the shape is continually changing. This occurs as the result of extension of pseudopodia in one direction, which movement must be accompanied by their withdrawal from other parts of the body. In this way, by an orderly extension of pseudopodia primarily on one side, locomotion may be effected, since the ectoplasm adheres to the surface of the mud sufficiently to prevent any 'back-slip'. The mechanism of extension of pseudopodia must be considered a little more fully. It used to be maintained, principally as a result of the work of Jennings, that the movement of *Amoeba* resembled that of a rubber bag, filled with water and rolled along a flat surface. The water corresponded to the endoplasm, contained within an elastic ectoplasm. But the ability of an amoeba to extend pseudopodia even when locomotion is impossible, as when suspended in jelly, renders it unlikely that such is actually the case. It is now realised that during locomotion endoplasmic granules can be seen moving in the direction of extension of the pseudopodium, whilst inclusions of the ectoplasm remain stationary. Further, the ectoplasmic layer over the pseudopodium shows no diminution in thickness. The ectoplasm cannot therefore be a rigid sheath, but instead it is maintained that ectoplasm is actually generated from endoplasm. When a pseudopodium is being withdrawn, as must always accompany the obtrusion of a new one, the reverse occurs, ectoplasm being converted into endoplasm. This conclusion rests upon the fact that there is no movement of ectoplasmic inclusions, whilst the ectoplasm in the region of withdrawal of a pseudopodium does not thicken. Since there is now less surface to be covered in that region the ectoplasm has presumably disappeared as a result of conversion into endoplasm, granules in which can be seen moving away from the erstwhile pseudopodium. This streaming motion of the endoplasm is also of great importance in the circulation of food-vacuoles. Amoebae frequently round themselves off and float,

particularly during periods of digestion.

Although the above observations have gone some way towards accounting for the mechanism of extension of pseudopodia, they do not solve the problem of the underlying causes. The protoplasm of *Amoeba*, as with all protoplasm, is essentially colloidal, the ectoplasm being in the gel state and the endoplasm in the sol state. When a pseudopodium is to be extended the ectoplasm changes from gel to sol, thus softening. The process of ectoplasmic contraction which follows forces out the endoplasm at this point, and as the extension occurs the surface layer returns to the gel condition. This is equivalent to saying that endoplasm changes into ectoplasm at the surface of an extending pseudopodium. It is probable that the contraction of the ectoplasm, mainly at the posterior end, is due to changes in shape and orientation of protein molecules forming the limiting layer, though it still remains to discover what occasions these changes.

But locomotion in *Amoeba* is not without reference to environmental conditions. If a pseudopodium, on extension, should come into contact with a foreign body, such as a grain of sand, it is retracted and a new one is pushed out in a changed direction. This means that the general protoplasm of *Amoeba* has the power to perceive nervous messages, or stimuli, over the whole of its surface, since at whatever point a pseudopodium is extended it will exhibit this reaction. Furthermore, the ability to conduct the impulse generated by the stimulus must also exist to promote the extension of new pseudopodia. The whole process has particular reference to pseudopodia, since it is these structures which normally perceive the stimulus, whilst it is also their formation which is accordingly modified. This property of response to particular conditions in the environment is known as **irritability**. But this characteristic is not highly developed in *Amoeba*, for, though its pseudopodia are withdrawn from stationary grains of sand, these foreign bodies are frequently engulfed if they are in motion. The significance of this is explained below.

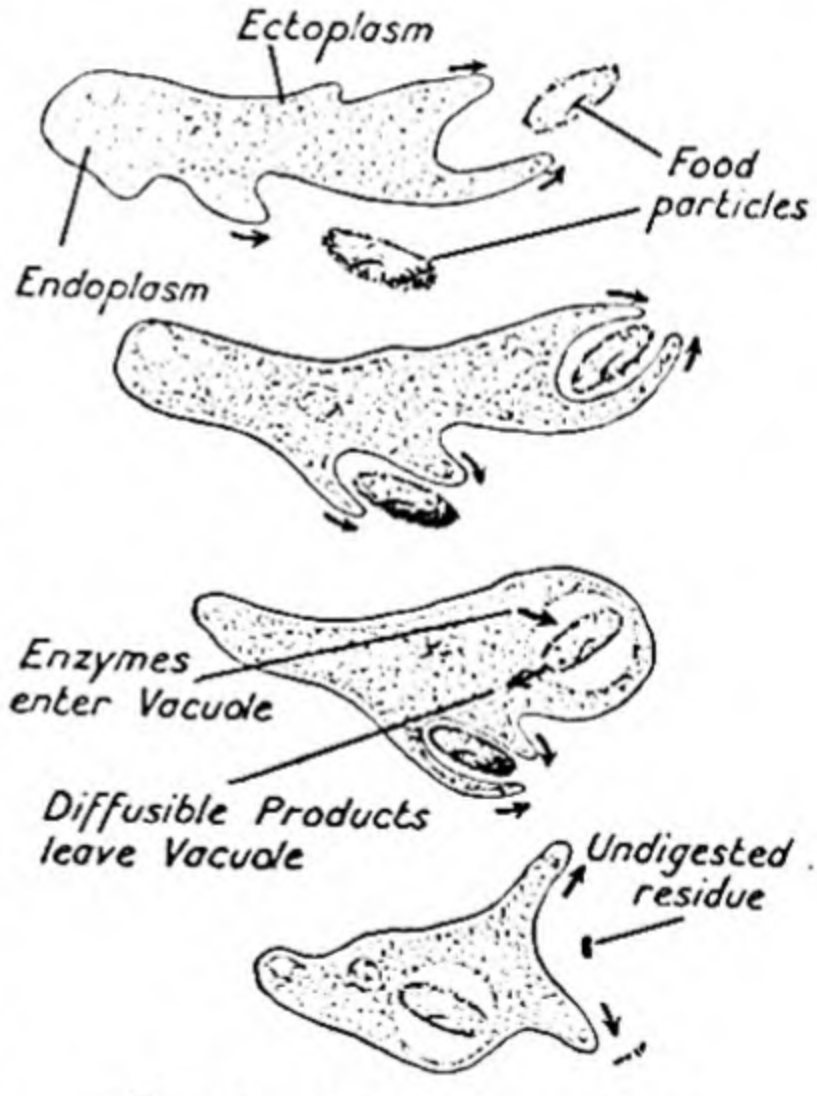


FIG. 2 – *Amoeba*. Ingestion.

Young amoebae live on minute ciliates or Algae (see Chapter 9), which are present in the water, whilst older individuals feed largely on rotifers. When the animal makes contact with such a body its response is

quite different from that which is elicited by a stationary grain of sand, for a number of adjacent pseudopodia, forming a *food cup*, at once commence to flow round the prey until the latter is eventually completely engulfed. This process is termed **ingestion**, and results in the inclusion of a small drop of water with the food, the whole constituting a food vacuole. The majority of the organisms affording the food of *Amoeba* are motile, being provided with a single flagellum (page 643), or a pair of such structures, by means of which locomotion is effected. It is probably as a result of this that a moving grain of sand may also be engulfed. *Amoeba* also exhibits some sensitivity to light. If suddenly illuminated it moves away from the source, possibly by the inhibition of pseudopodium formation on the illuminated side. The general result of such responses appears to be to maintain the animal in diffuse light of low intensity.

Ectoplasm

The ectoplasm, of which there is a continuous layer covering the whole surface, permits oxygen to enter the endoplasm, and carbon dioxide, produced as a result of respiration, to escape from it. It is this layer which is responsible for the limited powers of perception of stimuli exhibited by the animal. Its function in connexion with the extension of pseudopodia has already been described, whilst its reaction to the passage of water and solutes is discussed below.

Endoplasm

The primary function of the endoplasm is the digestion of food. The food vacuoles referred to above are circulated through the endoplasm, where their contents undergo hydrolysis, assisted by enzymes (page 389) secreted by the endoplasm. The liquid contents of the food vacuoles are at first acid, but at a later stage become alkaline. As a result the nutritious portion of the food is dissolved so that it can be absorbed and built up by *Amoeba* into its own body-substance. The insoluble matter which remains is cast out of the body through the ectoplasm. Also in the endoplasm are nutritive spheres and crystals. The former are bluish in colour and consist of material analogous to glycogen, enclosed within a pellicle and lying in a small vacuole. They are concerned with storage and disappear during sporulation (see page 8). The crystals are of shapes characteristic of the various species of *Amoeba*. Two organelles of the endoplasm deserve separate mention.

Contractile Vacuole

The contractile vacuole is fixed in position, adhering to the ectoplasm. The endoplasm of *Amoeba* contains osmotically active substances, and since the limiting layer acts virtually as a semi-permeable membrane (although not quite perfectly so, for limited diffusion of solutes does occur) water enters the endoplasm by osmosis. This accumulates in the

contractile vacuole, though actual transfer to this space must involve expenditure of energy, for it operates against the osmotic pressure gradient. Eventually the fluid contents of the vacuole are expelled through the adjacent point in the ectoplasm, and accumulation of water re-commences. Some nitrogenous waste substances get carried into the contractile vacuole and are thus eliminated, but this does not imply that this organelle is excretory. This aspect of its function is purely incidental, its major importance being as an osmo-regulator. The fact that a contractile vacuole is not present in comparable marine forms, where the sea-water and endoplasmic fluids are practically isotonic, is evidence of this. There is no doubt that the greater part of dissolved nitrogenous waste escapes by diffusion through the ectoplasm.

Nucleus

The nucleus exercises control over the life-processes of the animal. The ones mainly affected seem to be digestion and the consumption of oxygen. It can thus be inferred that the nucleus regulates the formation and activities of enzymes. Its size relative to that of the remainder of the body is a very important factor, and the nucleus itself is the first region to become concerned in the process of reproduction. In structure it consists of a central, dark-staining body, termed a karyosome, with a collar bearing granules of chromatin between it and the enclosing nuclear membrane. It is an elastic body and its shape is continuously changed as a result of the flowing movements of the endoplasm. *Amoeba* differs from higher animals and plants in that at no time is the process of growth exactly neutralised by that of wear and tear, so that the organism must be continuously increasing in size. But as this occurs the ratio of surface-area to volume must decrease. Now the surface is important in that it allows gaseous exchange of oxygen and carbon dioxide to occur, and that such respiration is essential to the life of animals and plants will be seen later (Chapter 24). There is therefore a minimum value for the ratio of surface-area to volume, below which respiration cannot continue sufficiently rapidly. When this value is reached the nucleus undergoes division into two identical halves by a modified form of mitosis (page 311). Following this the cytoplasm (*i.e.* the protoplasm other than the nucleus) constricts into two halves, the division occurring in such a way that each portion of cytoplasm contains

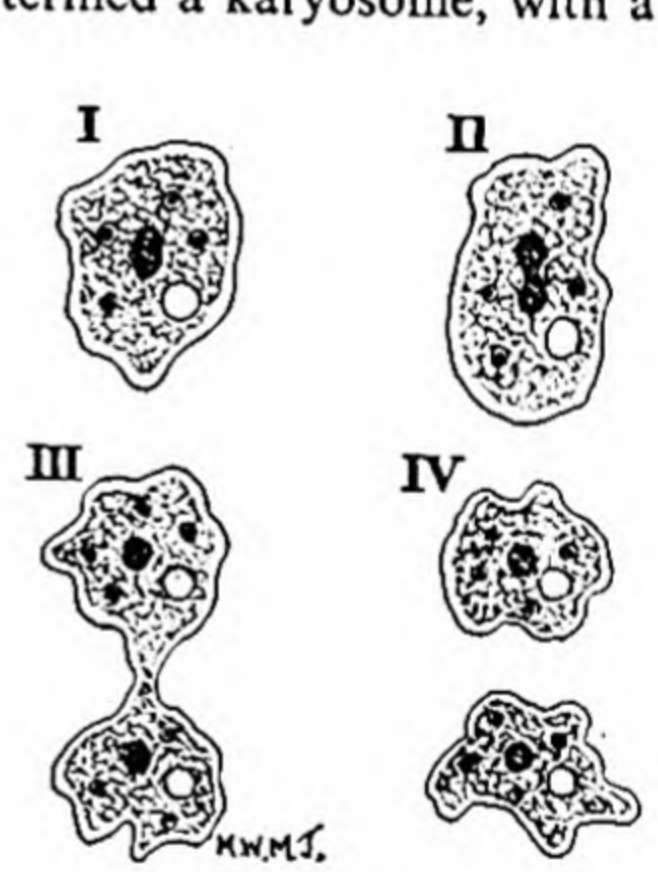


FIG. 3 – *Amoeba*. Binary fission.

one of the products of division of the nucleus. It is believed that the cleavage furrow of the cytoplasm always appears first at the posterior end (see page 4). This is the way in which *Amoeba* effects its reproduction, and it is known as **binary fission,** which can be completed in as little as fifteen to twenty minutes. Though, as pointed out above, the surface-volume ratio is important in determining the time and frequency of division, there is also an internal factor to be taken into account. Such physiological conditions as the presence and activity of respiratory and other enzymes are obviously important, since surface-volume ratio is by no means the same for all animals. Little is known of this factor.

Sporulation

In old amoebae a new phase in the life-history is encountered, for they have lost the power of undergoing binary fission. Instead, the nucleus may be seen to fragment and around each portion a minute mass of cytoplasm aggregates. The body so formed secretes a resistant cyst about itself and becomes a **spore**. Thus an old amoeba may contain several hundred spores, and eventually it disintegrates to set them free. In favourable conditions the spores may hatch. First a pulsating vacuole may be observed within the spore, which increases in size by the absorption of water. A very small infant amoeba – termed an *amoebula* – emerges and is seen to possess a single pseudopodium. Presently it becomes stellate and floats in the water. In this way some local dispersal may be effected. At this stage the amoebulae have many predators, but those which survive eventually assume characteristic shape and sink to the bottom of the pond, each to develop into a new adult. Thus sporulation affords a means of survival during periods of adversity, for the spores are capable of withstanding low temperature and periods of desiccation. Since they may be blown by the wind they also provide a mechanism for establishing new habitats.

2. PARAMECIUM

Paramecium caudatum, known from its shape as the Slipper Animalcule, is a Protozoön found in water containing decaying vegetable matter. A culture may readily be prepared by leaving hay for some days in water taken from a pond known to contain *Paramecium*, the hay serving as a source of food for bacteria upon which *Paramecium* preys. The animal is just visible to the naked eye, but a microscope is necessary to reveal details of its structure.

Structure

The 'anterior' end of the animal – *i.e.* the one which leads in locomotion – is slightly blunted, whilst the so-called 'ventral' surface is flattened. Starting to the left of the anterior end and curving into the 'mid-ventral'

line to run for some two-thirds of the length of the animal is a shallow **oral groove**, leading into a deep, backward-directed **gullet**, or **cytopharynx**. At the base of the gullet is naked endoplasm and this constitutes the **mouth**, or **cytostome**. The whole body is covered with **cilia**, each of which is a minute protoplasmic projection. As in *Amoeba* the protoplasm of which the body is composed is divisible into a clear, peripheral **ectoplasm** and an inner, granular **endoplasm**. The ectoplasm is further differentiated into a superficial **pellicle**, secreted by the ectoplasm and overlying a **cortex** within. *Paramecium* differs from *Amoeba* in that embedded in the endoplasm are two nuclei. One of these is large and termed the **meganucleus** (or **macronucleus**), whilst the other, lying close to it, or even embedded in it, is much smaller and is known as the

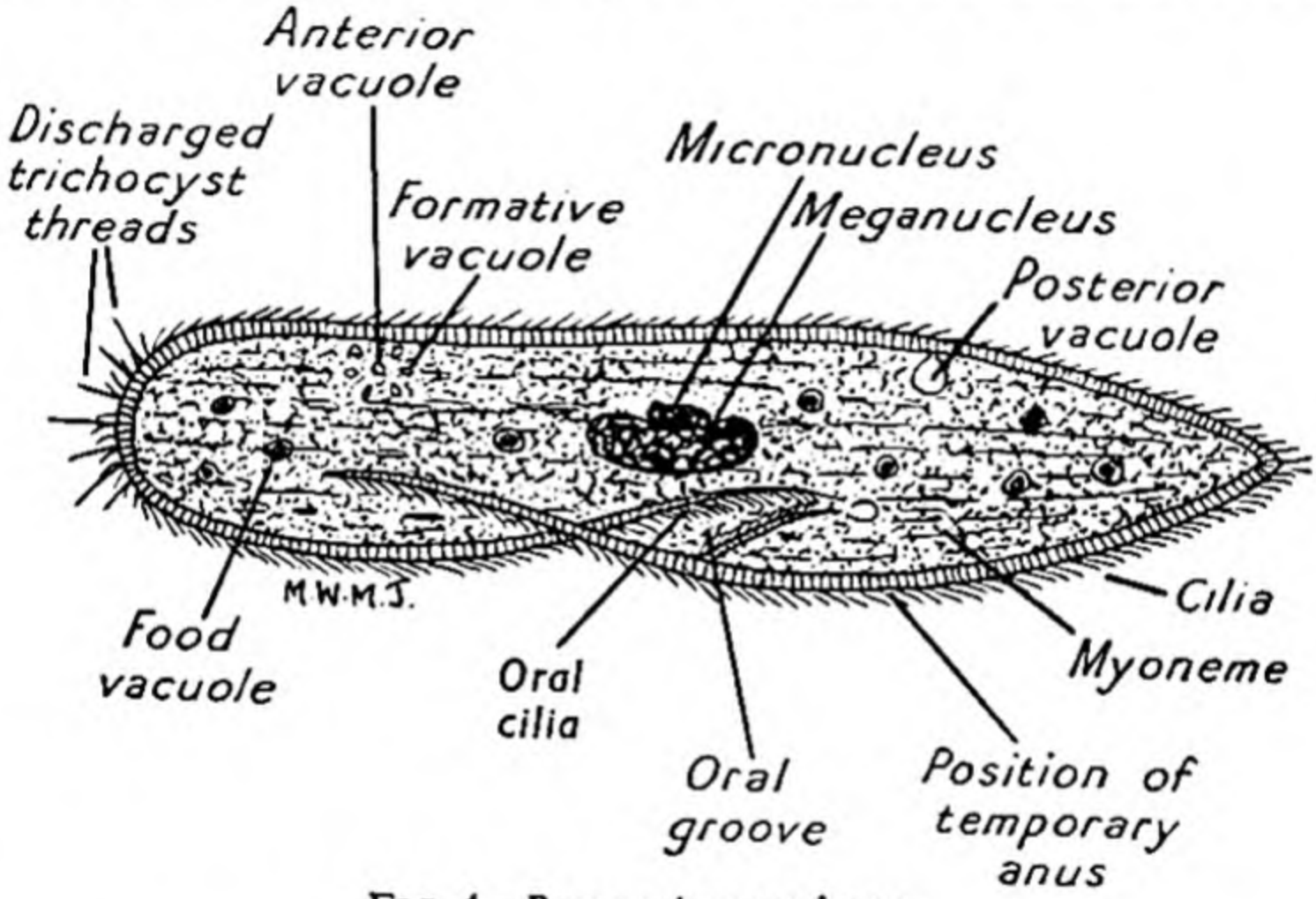


FIG. 4 – *Paramecium caudatum.*

micronucleus. There are also to be found in the endoplasm two **contractile vacuoles**, one at either end. Surrounding each of these is a number of contributory channels, termed **formative vacuoles**. Near each contractile vacuole the pellicle is softened.

Ectoplasm

The pellicle is divided into a number of minute, roughly rectangular pits. Opening into the ridges between pits are small bodies, termed **trichocysts**. Upon contact with foreign substances delicate threads are discharged from their openings. These threads are used either to effect temporary anchorage or to warn off would-be predators. From the centre of each pit there project two cilia. Every cilium terminates within the ectoplasm as a swollen body, known as the **basal granule**, whilst the cilium itself has been shown, with the aid of the electron microscope, to

consist of eleven discrete fibres, of which two form a central axis. The cilia covering the surface of the body effect locomotion, and the direction in which the animal is propelled is regulated by environmental conditions. These are described on page 453.

In connexion with the ciliary locomotion of *Paramecium* a phenomenon known as **metachronal rhythm** may be considered. The cilia covering the surface all normally beat at the same rate, but not at the same phase. Any given cilium is slightly ahead in its beat of the one next behind it, so that the movement of a band of cilia viewed collectively presents the same undulating appearance as the waves passing across a

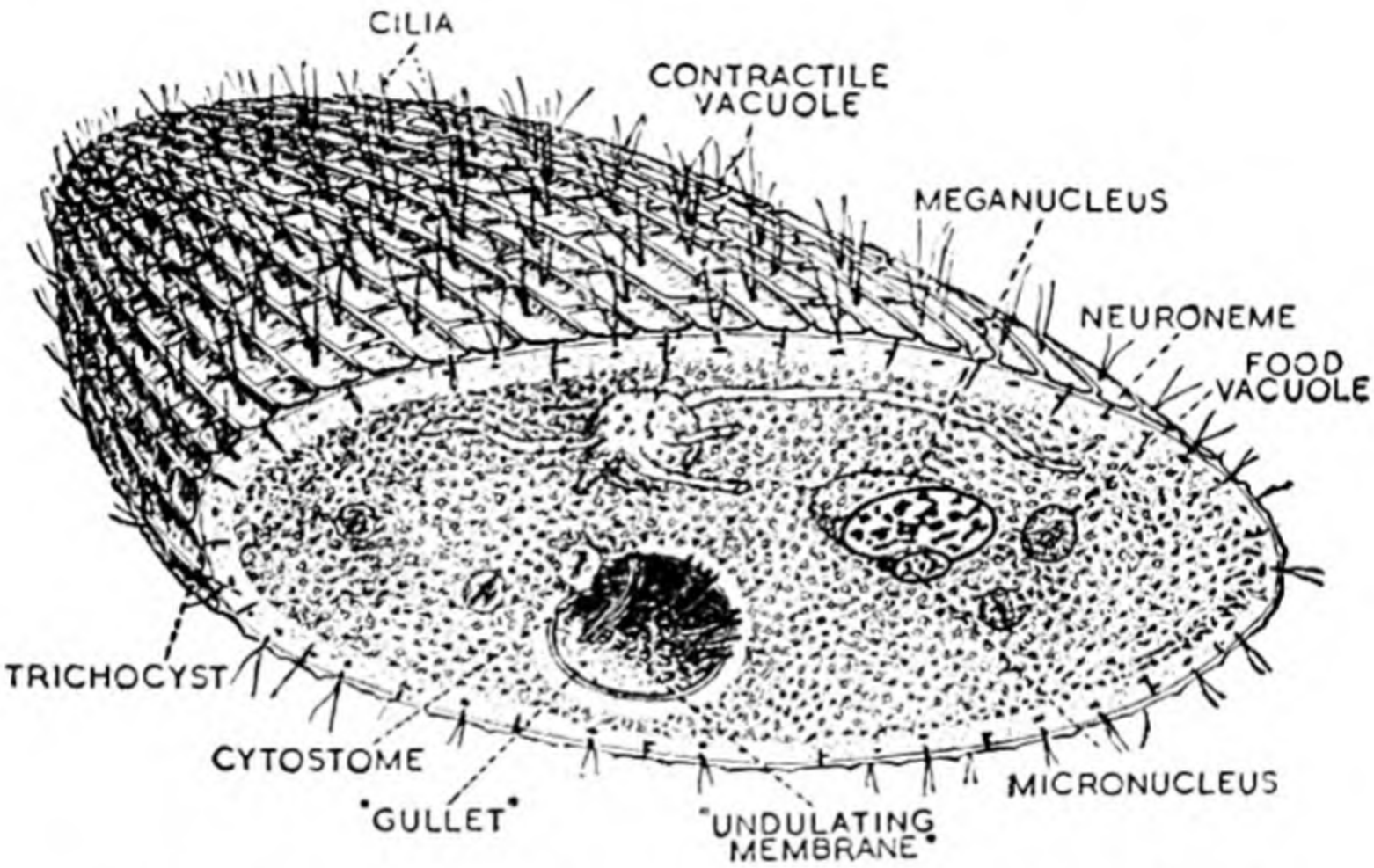


FIG. 5 – *Paramecium*. Cut through to show internal structure. (From 'Animal Biology', by A. J. Grove and G. E. Newell. University Tutorial Press.)

field of corn in a breeze. Every cilium makes its effective stroke obliquely backwards to the right. If this be resolved into its two components – one longitudinal to the rear and one horizontal to the right – it will be seen that the animal is at once propelled forwards and rotated in an anti-clockwise direction about its antero-posterior axis. Now the cilia in the oral groove beat more strongly than those elsewhere on the surface. The result of this, combined with the axial rotation already referred to, is that the actual *path* traced by the animal during forward movement is in the form of a spiral.

Normal control of this complex pattern of ciliary behaviour is believed to be exerted by a system of fibres, or **neuronemes**, in the cortex and with which the basal granules are connected. These neuronemes all converge

upon a single, granular **motorium** near the cytopharynx. Thus the neuronemes may well be analogous to the nerves of higher animals, with co-ordination based upon the motorium.

Deeper in the cortex is a system of longitudinal, contractile threads, known as **myonemes**. These are responsible for a limited degree of change of shape by the animal.

In addition to the cilia covering the surface there are two or three rows of cilia hanging from the roof of the cytopharynx. These beat in unison and collectively constitute what is sometimes, though inaccurately, termed the *undulating membrane*.

Finally it should be noted that the ectoplasm, including the pellicle, is sufficiently permeable for the inward diffusion of oxygen and the outward diffusion of carbon dioxide and soluble waste matter. Thus, as in *Amoeba*, respiration and excretion take place without any special mechanism being involved.

Endoplasm

As in *Amoeba*, the endoplasm contains numerous food vacuoles, in which lie particles in various stages of digestion. The food of *Paramecium* consists principally of Bacteria. As a result of the combined ciliary activity a cone of water, containing suspended food particles, is driven in the direction of the cytopharynx, along which the said particles are propelled by means of the bands of cilia in the roof, eventually to reach the cytostome, where ingestion occurs. These particles, together with a drop of water, are finally completely enclosed by the endoplasm, and the food vacuole so formed is subsequently circulated about the body on a fairly regular course, the contents being digested as in *Amoeba*, passing through first an acid, and later an alkaline, phase. An important storage substance, known as glycogen, also occurs in the endoplasm. Glycogen is a carbohydrate (page 369), chemically somewhat similar to the starch occurring in plants. It is found abundantly in the liver of vertebrates.

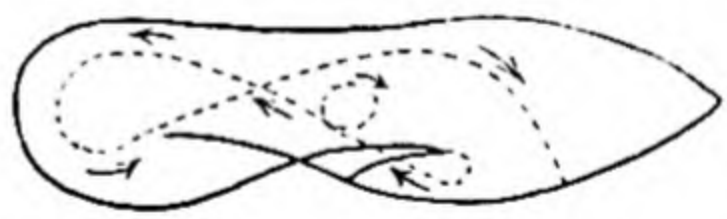


FIG. 6 – *Paramecium*. Diagram to show the path taken by a food-vacuole.

Osmo-regulation is achieved on the same principle as in *Amoeba*, but with slightly more elaborate apparatus. As the contractile vacuoles are filling, as a result of endosmosis through the ectoplasm, pear-shaped formative vacuoles (page 9) appear around them. As each contractile vacuole itself discharges, the formative vacuoles themselves coalesce to originate the next contractile vacuole, though as yet small, whilst slit-like formative vacuoles re-appear. The posterior vacuole pulsates the more rapidly of the two, possibly due to the proximity of the cytostome, where endosmosis may be more effective.

Nuclei

The function of the meganucleus is the control of the life-processes of this non-cellular organism. Like the micronucleus its division precedes the constriction of the cytoplasm when reproduction is being effected by binary fission. This process occurs two or three times a day in a healthy culture. But on occasions a much more complicated phenomenon is observed, in which the behaviour of the micronucleus is of primary importance. The process concerned is known as **conjugation**, the significance of which is described in Chapter 32.

Conjugation

Two individuals first come together by their ventral surfaces, and their protoplasm becomes continuous across a narrow bridge. The two individuals concerned are now known as conjugants. The micronucleus in each conjugant divides twice, thus forming four nuclei. Three of them remain inactive and eventually disintegrate, whilst the fourth divides again, so that each conjugant now contains two nuclei. Of these one passes from each conjugant into the other, so that there is effected an exchange of nuclear material. The nucleus passing from one conjugant into the other is termed the **migratory nucleus**, whilst the **stationary nucleus** is the one remaining in the conjugant within which it originated.

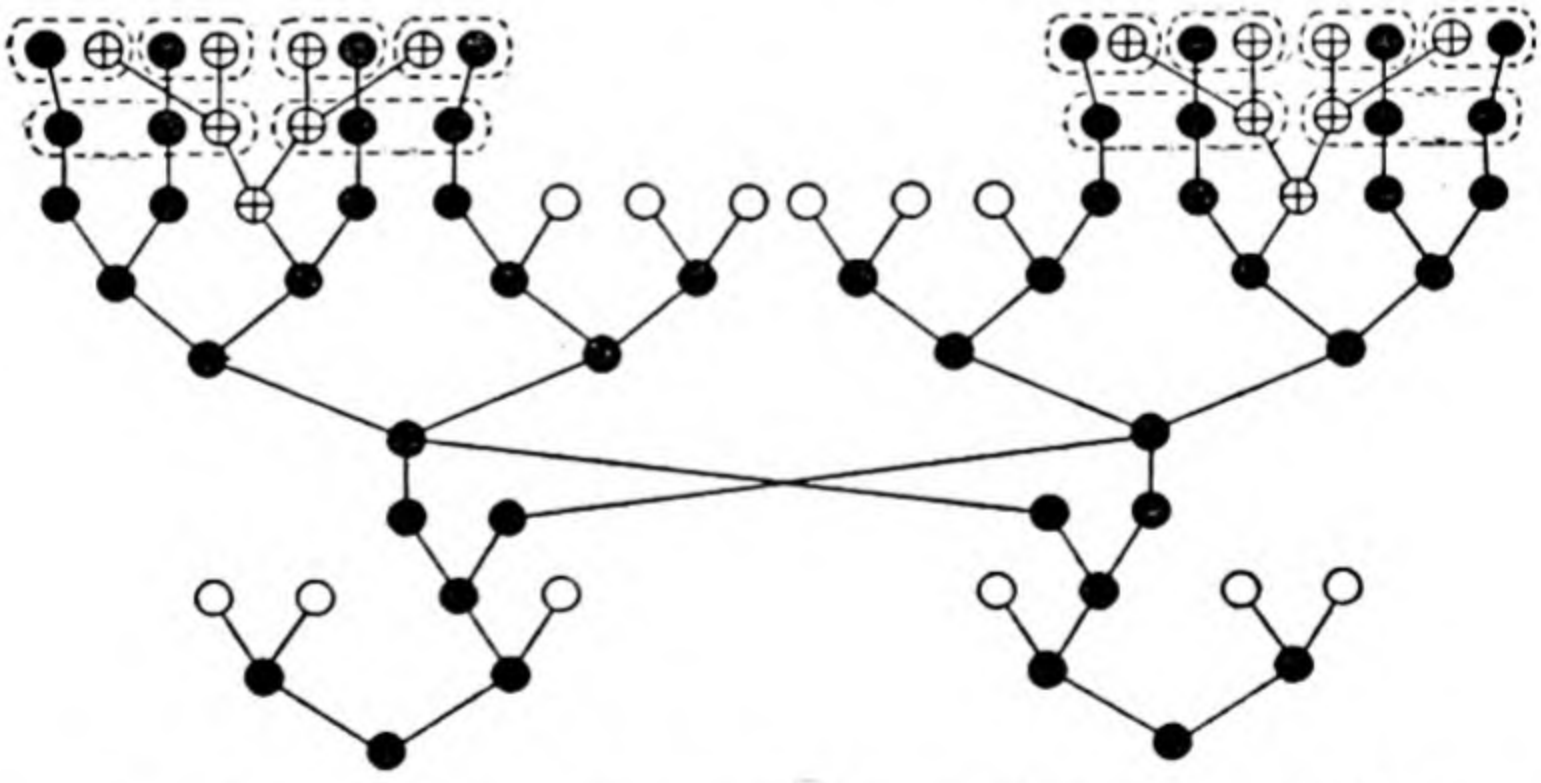


FIG. 7 – *Paramecium*. Diagram to show nuclear behaviour during conjugation. Nuclei left clear are resorbed into the cytoplasm, whilst those marked with a cross re-divide in the closing stages of the process, as shown.

A very important feature of conjugation now follows, for the migratory nucleus of each conjugant fuses with the stationary nucleus of the other. This is a characteristic of sexual reproduction, exhibited by the vast majority of higher animals and plants. The conjugants now separate,

the meganucleus of each having by this time disintegrated and disappeared. The fused nucleus in each ex-conjugant now divides to form eight daughter nuclei, three of which become resorbed into the cytoplasm. The cytoplasm of each ex-conjugant now becomes constricted into two halves. Four of the five nuclei present undergo no further division for some time, but the fifth divides at the same time as the cytoplasm, so that each daughter mass of cytoplasm comes to contain three nuclei – two of the undividing four and one product of division of the fifth. The latter nucleus now divides again in each daughter cell, and the cytoplasm becomes so constricted that each of the four masses produced by division of each ex-conjugant contains two nuclei, namely one of the undividing four and one product of the double division of the fifth. In each case the former becomes the meganucleus and the latter the micronucleus of a new paramecium. In all, therefore, a total of eight new individuals result from the process of conjugation. The significance of conjugation is mentioned on page 563.

In conclusion two additional points should be noted, both associated with the life-history of *Paramecium*. The first is that little or nothing is known about the dispersal of this animal from one habitat to another. Even if cysts are formed they have never been identified.

The second concerns the existence of two different 'strains' of *Paramecium* – the 'killers' and the 'sensitives'. The former secrete a toxic substance, *paramecin*, which paralyses the locomotory and feeding mechanism of the latter. The matter of the inheritance of these characteristics is discussed on page 587.

PARASITIC PROTOZOA

The two members of the phylum Protozoa described above are free-living organisms, obtaining their food from the water in which they are contained. But a number of Protozoa live more or less permanently within the bodies of other animals. An animal or plant which does this is said to be a **parasite**, whilst the organism accommodating it is termed its **host**. (For further discussion of the phenomenon of parasitism see Chapters 23 and 39.) Two selected examples of parasitic Protozoa will be described, after which certain general conclusions will be drawn.

I. MONOCYSTIS

Amongst the reproductive organs of the earthworm are three pairs of large sacs, known as *vesiculae seminales*, in which the spermatozoa ripen. The cavities and walls of these sacs are frequently inhabited by a parasitic Protozoön, known as *Monocystis*, of which there are two species, commonly found together. The phenomenon of parasitism and the characteristics of organisms which practise it are discussed on page 50.

Monocystis magna, as its name suggests, is the larger of the two, and is actually visible to the naked eye, normally occurring attached to the lining of a vesicula seminalis or the funnels of the vasa deferentia. The other species, *Monocystis lumbrici*, lives freely within the cavity of this organ. The bodies of members of both species are long and narrow, with the cytoplasm clearly differentiated into ectoplasm and endoplasm. The surface is covered with a pellicle, beneath which, as in *Paramecium*, is a layer of contractile protoplasm, termed the **myocyte**. At one end of every member of the *magna* species is an indistinct, knob-like structure, important for effecting attachment to a host cell of the lining or a funnel. The nucleus is a large, spherical structure, and contained within the endoplasm is a great deal of a carbohydrate storage product known as **paramylum** (or paraglycogen), a substance somewhat similar to glycogen (page 371). There is no contractile vacuole present.

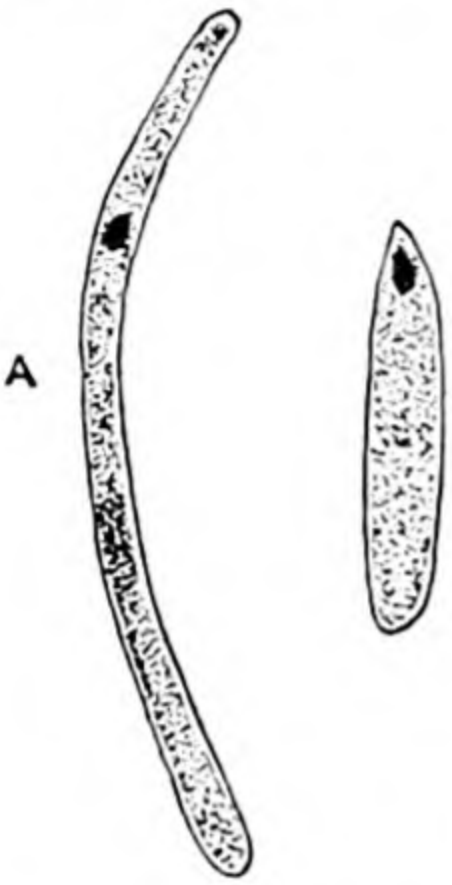


FIG. 8
A., *Monocystis magna*; B., *Monocystis lumbrici*. (From 'Manual of Zoology', by L. A. Borradaile. O.U.P.)

Having no pseudopodia or gullet the parasite absorbs through its body-surface the food intended for the developing spermatozoa, and in a similar manner waste products escape in solution. *Monocystis* feeds by the absorption of nutriment from the fluid contents of the vesiculae seminales, any necessary digestion being effected with the aid of enzymes diffusing from the surface. Oxygen, supplied by the blood of the host, diffuses inwards, whilst carbon dioxide and nitrogenous waste diffuse outwards. The absence of a contractile vacuole indicates that no osmoregulation is required, since apparently the fluid in the vesiculae seminales is isotonic with the endoplasmic fluids of the parasite. Some slight powers of locomotion are lodged with the *lumbrici* species on account of the presence of the myocyte.

Life-history

It will at once be apparent that one of the most vital problems confronting a parasite is the infection of new hosts, since the life of a single parasite is terminated on the death of its host. Accordingly it is commonly found that the life-history – the events occurring between the appearance of one adult and the maturation of the succeeding generation of adults to which it gives rise – is complicated, and *Monocystis* is no exception to the rule. The adult form above described is known as a **trophozoite**, and these, now termed **gametocytes**, come together in pairs, each pair becoming enclosed within a double-walled **gametocyst** (Fig. 9, A). No fusion

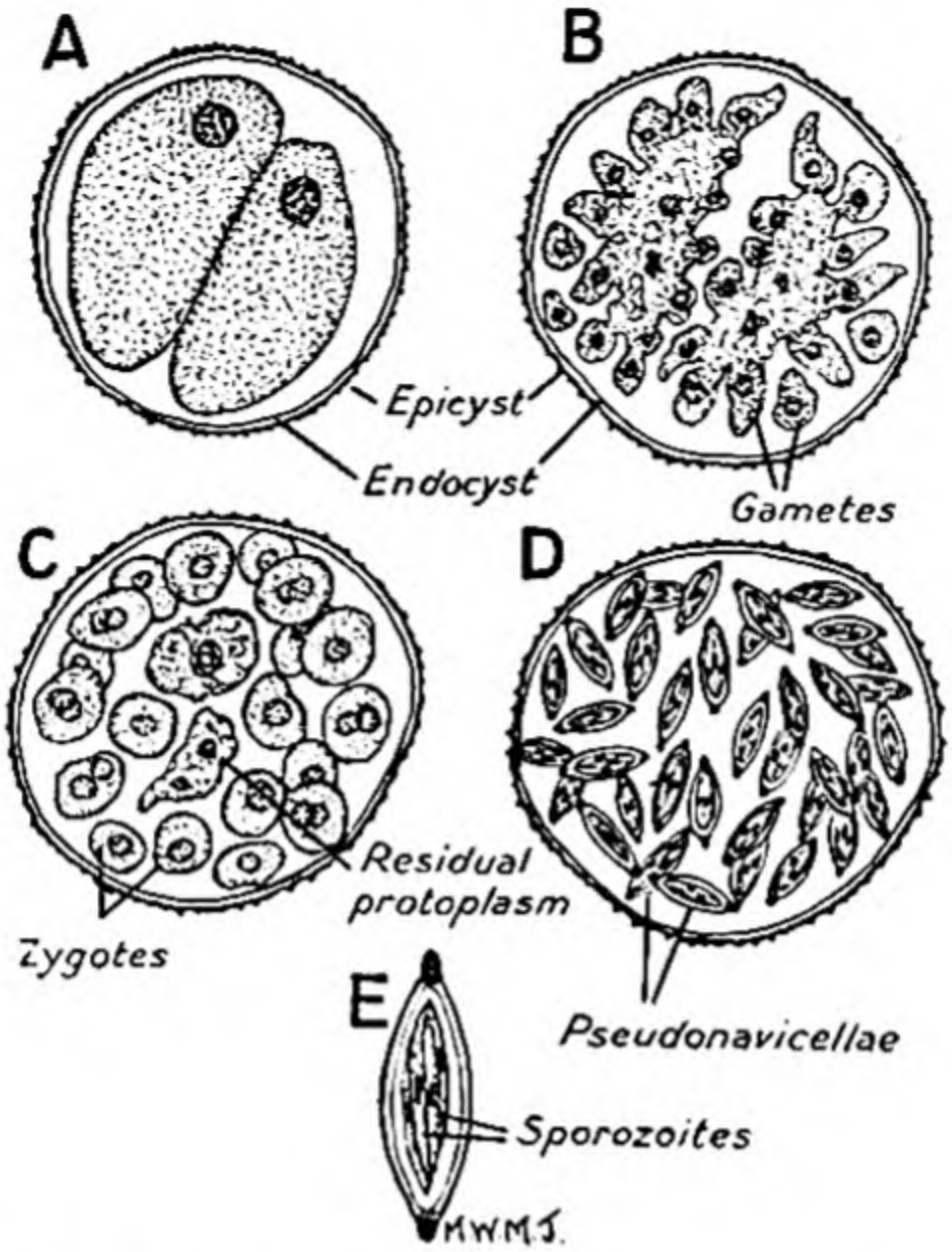


FIG. 9 – *Monocystis*. Stages in the life-history.
A., Two gametocytes in cyst; *B*., Formation of gametes; *C*., Fusion of gametes to form zygotes; *D*., Pseudonavicellae in cyst; *E*., Single pseudonavicella, containing eight sporozoites.

occurs at this stage, but each member of a pair undergoes multiple fission in much the same manner as an encysted amoeba. Eventually there remains a large number of fragments of cytoplasm, each with its own nucleus, and these are nourished by a residual mass of enucleate cytoplasm (Fig. 9, B and C). These small cells, or **gametes**, conjugate in pairs, and the uniting elements are derived from different trophozoites. In *M. lumbrici* the gametes actually differ in shape, the 'female' being round and the 'male' pear-shaped. The product of fusion of these two cells forms a zygote (page 556), and each zygote now becomes separately surrounded by a **sporocyst** to form what is known as a **pseudonavicella**, whose living contents constitute a **sporoblast** (or sporont). Each sporont then undergoes three successive divisions to form eight minute, sickle-shaped **sporozoites** (Fig. 9, E). Thus at this stage there is present one comparatively large gametocyst containing many smaller capsules (pseudonavicellae) within each of which are eight sporozoites (Fig. 9, D). These latter undergo no further development as long as they remain within their host, but escape is usually effected by the death and

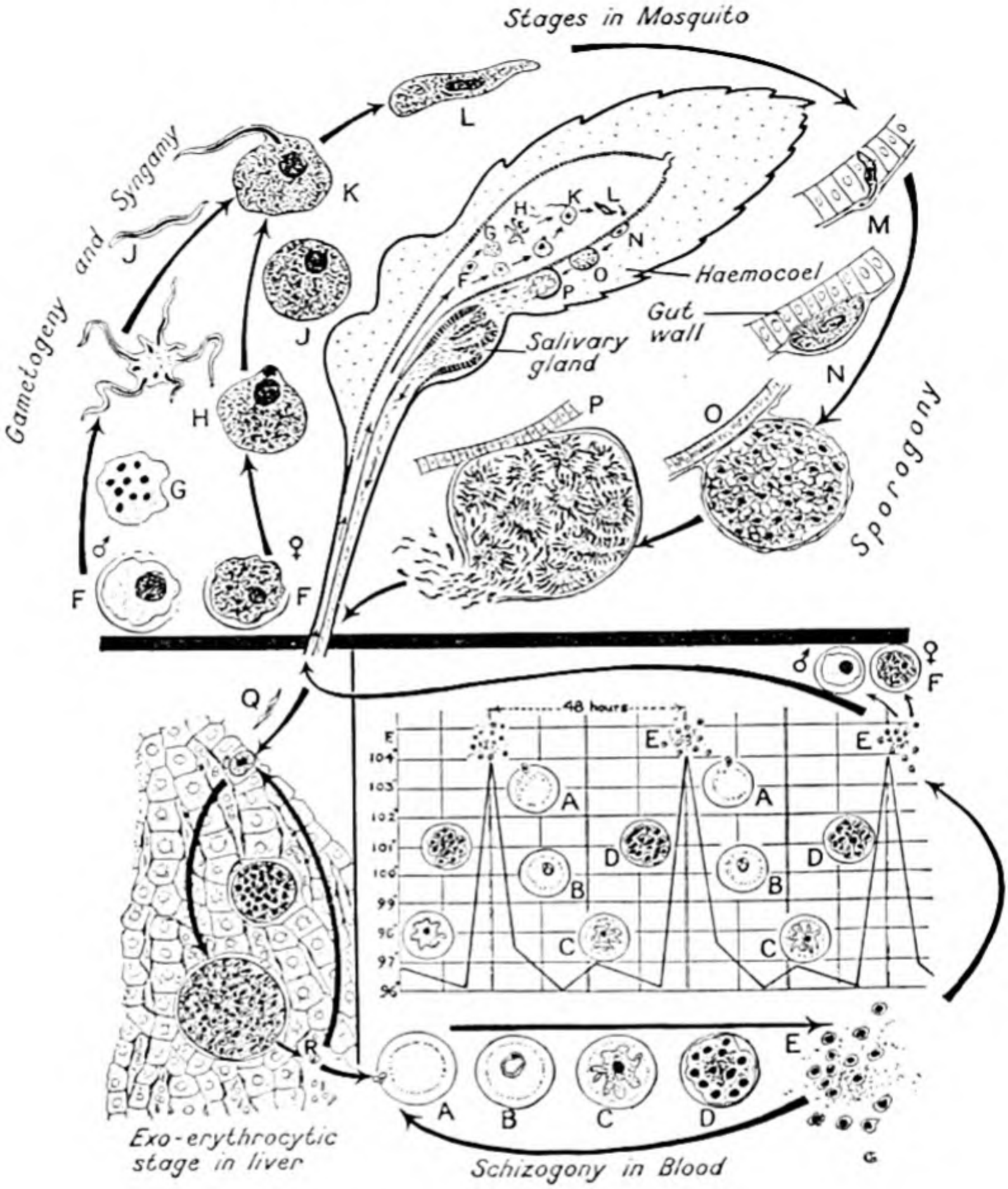


FIG. 10 (Key at foot of page 17.)

decay of the host earthworm or possibly by its being eaten by a bird, through whose alimentary canal the pseudonavicellae may pass unharmed to be shed with the faeces. If and when contaminated soil is taken into the alimentary canal of another earthworm the pseudonavicellae are dissolved, thereby liberating the sporozoites. Each makes its way through the tissues of its new host until it reaches the vesiculae seminales, where it matures to form a trophozoite, as a result of its penetration of a sperm

mother-cell (a cell which, by division and differentiation, would have eventually given rise to sperms). Such a cell normally proceeds with the initial stages of spermatozoa development (page 63), but fails to complete its mission. Young trophozoites may, in fact, often be seen to be covered with the tails of withered spermatozoa, creating the illusion of a ciliated surface:

Thus the life-history may be summarised as follows:

2 trophozoites→2 gametocytes→x pairs of gametes→x zygotes

↓

$8x$ trophozoites←$8x$ sporozoites←x pseudonavicellae←x sporoblasts

The formation of the full ($8x$) number of trophozoites obviously depends on the assumption that all the sporozoites reach a new host.

2. PLASMODIUM

Malarial fever in man is caused by the invasion of the body by a parasitic Protozoön, known as *Plasmodium* (or *Haemamoeba*). The adult form corresponds to the trophozoite of *Monocystis*. It lives within a red blood-corpuscle of its host, and is at first ring-like, owing to the presence of a large, though non-contractile, vacuole. There is present a single nucleus, and subsequently the vacuole disappears, whilst pseudopodia are extended. It feeds by the absorption of material through its surface, and eventually granules of pigment, formed by the decomposition of haemo-

15755

FIG. 10 – *Plasmodium*. Stages in the life-history. *A* – *E*, Schizogony in the blood, resulting in the release of further schizozoites into the blood-stream, as well as metabolic by-products, accompanied by fever and high temperature of the patient; repeated every 48 hours (in the case of the species of *Plasomdium* selected for illustration) and results in the destruction of a vast number of red corpuscles and in impending death of the patient; at this point a few products from *E* may become gametocytes (*F*), developing further (*F* – *J*) into gametes only if sucked into the gut of a mosquito; *K*, Fertilisation; the zygote (*L*) invades the gut wall of the mosquito and undergoes much multiplication and encysts (*M* – *P*); sporozoites are liberated by the bursting of the cyst (*P*) into the haemocoel of the mosquito and travel to the salivary glands; these sporozoites are discharged into the blood-stream of the next victim of the mosquito and a single sporozoite (*Q*) is seen entering the liver, where much multiplication occurs and probably dormant stages are retained, often responsible for a relapse by the patient many years after; on release from the liver (*R*) the parasites invade erythrocytes.
(In *P. malariae* the schizogony cycle occupies 72 hours, whilst in *P. falciparum* it is less regular; the sporogony cycle normally occupies 10 – 12 days.)

globin (page 434), may be identified. In this amoeboid condition it is known as a **meront** (or schizont), whilst its multiplicatory process which follows is termed **merogony** (or schizogony). Pseudopodia are now withdrawn, whilst the nucleus divides to form some sixteen daughter nuclei, each of which is enclosed within a small fragment of cytoplasm to form a **merozoite** (or schizozoite). The merozoites are at this stage congregated around a central, residual mass of cytoplasm. The merozoites are now liberated from their host cell by rupture of the latter's wall, and are distributed in the blood-stream, where they infect fresh corpuscles. The above cycle of changes is then repeated. According to the species of *Plasmodium* the time taken for the completion of this cycle varies from two to several days, and attacks of the fever coincide with the liberation of the parasites from the red blood-corpuscles, on account of the dissemination into the bloodstream at this time of toxic substances produced by the parasite. The regular recurrence of the fever, coinciding with the liberation of the parasites, assumes that all the parasites are at the same stage – *i.e.* they were all introduced at a single infection.

It is obvious that frequent repetition of this cycle results in a rapid increase in the number of parasites in the host. About a fortnight after the symptoms first appear, the parasites are so plentiful that either they are on the point of proving fatal to their host, or the powers of resistance of the host are resulting in the commencement of their destruction. In either case it is expedient that the parasite infect a new host. At this stage in the life-history a new type of individual makes its appearance: it is the **gametocyte**, formed by modification of the structure of the schizont. A gamont undergoes no further change whilst within the host, but the distribution of malaria is effected by the sucking of the blood of an infected person by a mosquito, of genus *Anopheles*, the female alone of which bites. Within this latter all the stages of *Plasmodium* are destroyed by digestion except the gamonts, which are themselves divisible into two groups, namely, male and female. The **female gametocyte** undergoes little change. A single nuclear division occurs, though one of the products retains almost all the cytoplasm, whilst the other remains practically naked and disappears. The former becomes a **megagamete** (or macrogamete). In the **male gametocyte** a few nuclear divisions occur in such a way that eventually some eight nuclei are arranged at the periphery of a residual mass of cytoplasm. A thread from each nucleus grows outwards to become enclosed in a very delicate layer of cytoplasm, and thus **microgametes** are formed. By the lashing of its 'tail' each eventually breaks loose from the residual cytoplasm into the cavity of the stomach of the mosquito. The megagamete, also in the cavity of the stomach, is penetrated by a microgamete, and the nuclei fuse, thus forming a zygote. This eventually elongates to form a worm-like organism (though still non-cellular), which pierces the endothelium (page 329) lining the stomach, within whose wall it settles down in the form of a cyst. At this

stage it is known as a **sporont**. It continues to absorb nourishment through the thin-walled cyst, and in consequence increases considerably in size, becoming visible from the outside of the stomach as a swelling. Within the cyst nuclear division proceeds rapidly, and each daughter nucleus thus formed acquires a covering of cytoplasm to form a **sporoblast**. From the surface of each sporoblast protoplasmic processes grow out, and into each passes a nucleus formed by division of the original sporoblast nucleus. Thus, within the sporont cyst there is a number of masses of protoplasm, to the periphery of each of which is attached a number of short, filamentous **sporozoites**, which are eventually set free from the residuum of cytoplasm around which they were collected. Eventually the sporont cyst bursts, liberating the sporozoites through the outer surface of the stomach into the body-cavity of the mosquito, from which they ultimately reach the salivary glands. When the mosquito subsequently sucks the blood of a man the juice which it injects into the wound is laden with these sporozoites, which thus initiate a fresh infection. Each sporozoite penetrates a red corpuscle and becomes a typical adult.

It was formerly believed that these sporozoites immediately attacked the red blood-corpuscles of the victim, but recently, investigations by N. H. Fairley, E. H. Shortt, *et alia*, have produced an important advance in our knowledge of the early stages in the development of malaria. Volunteers were infected with sporozoites and their blood then transfused to other (non-infected) volunteers. It was found that if the transfusion were performed within an hour of the original infection the disease subsequently appeared in the recipients. But if the transfusion were delayed until any time between one hour and eight days after infection, then the disease was not transmitted. This pointed conclusively to the existence of an exo-erythrocytic stage in the life-history of the parasite, for apparently the sporozoites had left the circulatory system to undergo developmental changes elsewhere. The site of this phase in the life-history was eventually located in the liver. Comparable experiments were performed on monkeys, using *Plasmodium cynomolgi*, closely allied to *Plasmodium vivax*, and similar results were obtained, whilst in birds other organs, including the skin and spleen, as well as the liver, appear to harbour the exo-erythrocytic stage.

The details of the changes undergone by the parasites during this incubation period have yet to be investigated, but it is apparent that herein lies the explanation of renewed bouts of malaria after long periods of remission, even when the patient has been removed to a climate where the disease does not normally occur. Furthermore, there is no known drug which will destroy the parasites during this incubative phase, though paludrine is believed to be partially effective. Thus medical treatment can at present do little more than suppress the symptoms during the erythrocytic stage in the life-history of the parasite.

Parasitic Features

By a careful study of the foregoing examples the attributes of a parasitic organism may be identified. In each case subsistence is derived from an individual living host. But in the mechanism of infection of new hosts there are important differences which do not, however, abrogate the existence of a general principle. The chief differences are as follows:

(i) There is no separate asexual reproduction in *Monocystis*.

(ii) In *Plasmodium* there is distinct differentiation of the gametes into male and female.

(iii) Part of the life-cycle of *Plasmodium* occurs in a different kind of animal, known as an intermediate host, from the one in which the harmful effects are exerted. In *Monocystis* the bird is not a true intermediate host, since no actual developmental stages in the life-history of the parasite are completed within it, nor is it essential to the spread of the parasite, if, in fact, it participates at all.

But in spite of these discrepancies certain fundamental characteristics of the life-history of a parasitic animal may be elucidated.

(i) There are several multiplicatory phases. Thus in *Monocystis* two will be observed, namely the division of the gametocytes to form gametes, and of each sporont to form eight sporozoites. In *Plasmodium* there are even more. Considerable multiplication by asexual methods occurs immediately upon infection and continues for some time afterwards. Each sporont subsequently gives rise to many sporoblasts, from each of which are liberated many sporozoites.

(ii) Resistant bodies are formed during the life-cycle to accommodate transference from one host to another. This is not well shown in *Plasmodium*, since at no time is the parasite not contained within the body either of its true or of its intermediate host. But in *Monocystis* the pseudonavicellae are important in protecting the sporozoites during the period between escape from one worm and entrance into the body of another.

Other Parasitic Protozoa

In conclusion mention may be made of a few other parasitic Protozoa, especially those of importance to man.

Entamoeba histolytica, known also as *Entamoeba dysenteriae*, is related to *Amoeba* and is parasitic in the large intestine of man, usually causing amoebic dysentery. It moves by means of a single, large pseudopodium and has no contractile vacuole. It penetrates the endothelial cells of the intestine, causing ulcers, and it may get carried in the blood-stream to the liver, where it is responsible for the formation of abscesses. Its food consists largely of erythrocytes (page 327), but nutrient fluids may be absorbed over the general surface. As well as reproducing by binary fission, it is also capable of encystment. The cyst is secreted by the adult

stage and thereafter the nucleus divides twice. If this body enters the alimentary canal of man the cyst is dissolved to liberate four young parasites and infection is accomplished. The transfer may be facilitated through drinking water or contaminated food, or through the excreta of flies.

Entamoeba coli. This animal hardly qualifies for the status of parasite, since it appears to exert no harmful effects, though living in the human large intestine. It is smaller than *E. histolytica*, which it otherwise resembles. It lives mainly on Bacteria found in the colon. Its life-history is similar to that of *E. histolytica*, except that in the encysting stage the nucleus divides three times to form a total of eight. Infection is accomplished similarly, although the cysts appear to be less resistant.

Balantidium coli is protozoan parasite, a ciliate and a near relative of *Paramecium*, which it resembles quite closely in structure. Of similar shape, it possesses a cytopharynx and cytostome, two contractile vacuoles (unusual in parasites), longitudinal rows of surface cilia and a mega- and micro-nucleus. It normally reproduces by binary fission, whilst conjugation has been observed. On occasions it encysts, and it is these cysts which facilitate transmission to new hosts. It is found most commonly in the intestine of the pig, where it appears to be harmless, but if it finds its way into the intestine of man it may cause dysentery. Once established here it may get carried in the blood-stream to other organs and set up abscesses.

The Trypanosoma constitute a further group of parasitic Protozoa. They are all essentially similar in structure and this common plan will first be described, after which reference will be made to two specific examples. In shape they are elongated, pointed at both ends and bearing a long flagellum at what must be described as the 'posterior' end, since the flagellum trails behind when the animal is moving. Along one side of the animal extends an undulating membrane, bordered by a continuation of the flagellum, whilst the whole body is enclosed within a pellicle. Associated with the base of the flagellum is a blepharoplast, probably controlling its movement, and a parabasal body. During the course of the life-history the typical form is variously modified by changes in shape and orientation of the organelles, but always it remains comparable with the 'adult' form.

Trypanosomes are typically blood-parasites and absorb nutrient fluids over their general body-surface. Diffusion of oxygen, carbon dioxide and nitrogenous waste occur as in other parasites described, whilst there is no contractile vacuole. Locomotion is effected by the movements of the undulating membrane and flagellum, as well as by some contractile activity by the body as a whole.

Trypansoma gambiense is responsible for the disease known as 'sleeping sickness' in tropical Africa. Transmission of the disease is due to bites from the tsetse fly, *Glossina palpalis*. Once blood from an infected person

has been sucked by the fly the trypanosomes multiply in the gut and eventually rather more slender forms appear. These migrate to the salivary glands where, after a further multiplicative phase, parasites of typical 'adult' form appear. These are ready to be injected into the next victim of the tsetse fly.

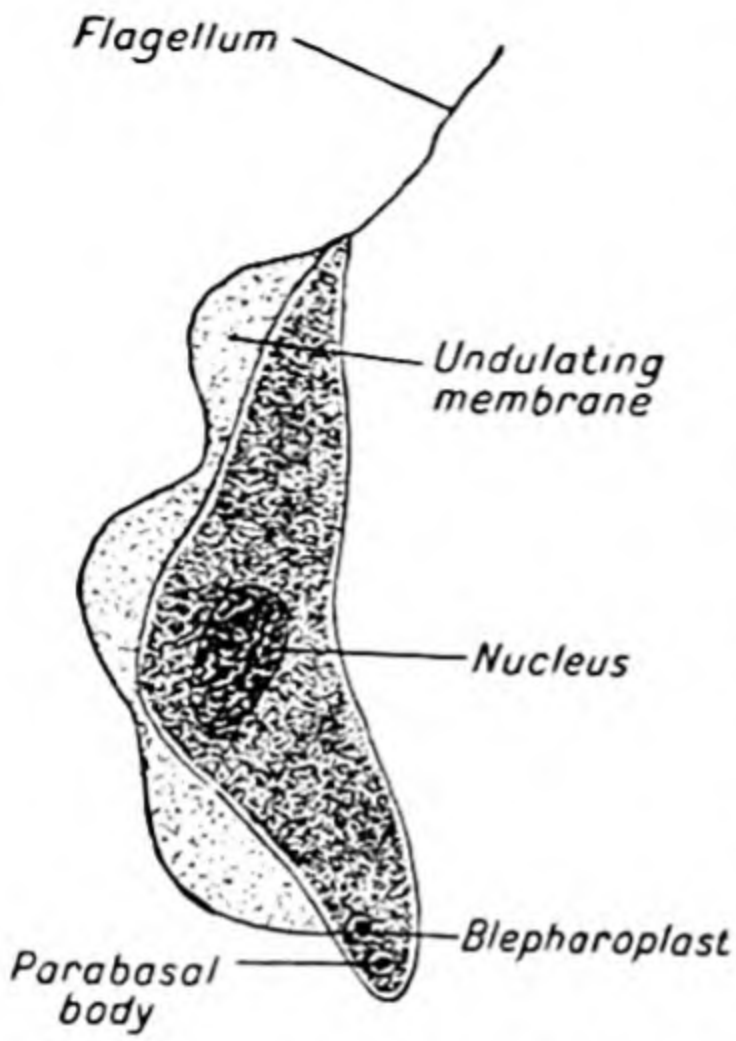


FIG. 11 – *Trypanosoma gambiense.*

Trypanosoma lewisi. The major host of this parasite is the rat. The blood of an infected rat is sucked by the rat flea and in the stomach of the latter they penetrate the cells of the endothelium, there to undergo a multiplicative phase. Once released into the cavity of the stomach these products of multiplication may either invade new endothelial cells or be passed along the gut to the rectum, where they undergo further multiplication. Eventually small 'adults' are discharged with the faeces of the flea and enter the body of the rat as the latter licks its fur. Thus the cycle is completed. It is a rather remarkable fact that rats become immune to attacks of this parasite, for after the blood has been infected for some time all the various forms die off.

Several other Trypanosomes causing diseases in tropical countries, both to man and his domestic animals, are known. An important factor in fighting these infections is the knowledge that, in many cases, wild game act as reservoirs for the trypanosomes, which abound in their blood-streams without exerting any harmful effects.

Control of Malaria and Sleeping Sickness

Though malaria is less severe in its effect than sleeping sickness it is of such wide distribution that its control is a matter of extreme importance. Before the stages in the life-history of *Plasmodium* were known the only method of fighting the disease was the administration of quinine to patients already infected. Since the parasites in the blood were in this way destroyed, including the gametocytes, the spread of the disease was in some measure minimised, though the treatment was essentially curative rather than preventative. Other drugs are now prescribed for the destruction of the parasite at various stages in its life-history. The initial presence of sporozoites is normally unsuspected, but once these reach the liver they may be immobilised by paludrine or primaquin. Schizozoites are susceptible to the influence of quinine or mepacrine, whilst chloroquine

is effective against the gametocytes. Combinations of these drugs may be administered not only to suppress the symptoms, but also to induce immunity. Once the significance of the mosquito as an intermediate host was realised a new method of attack was presented, aiming at the elimination of mosquitoes. The destruction of adults on anything approaching an adequate scale is not possible, but use is made of the fact that the eggs are laid in water. In many cases suitable ponds are filled in, whilst the larvae are prevented from maturing by the pouring of oil on to the surface of water where development is taking place. Since the larvae depend from the surface of the water by the expanded edges of tracheal tubes, the reduction in surface tension resulting from the addition of the oil causes them to drown. The destruction of larvae is further effected by the introduction into the ponds of fish, of which they form the staple diet. Thus with the enormous reduction in numbers of mosquitoes the extent of the disease has become considerably curtailed, since the parasites, in the absence of an intermediate host, are unable to complete their life-history.

Glossina presents no such convenient stage in development for destruction by man, and consequently no organised attacks can be made on it. Since its two most important species, *palpalis* and *morsitans*, are responsible for the distribution of Trypanosomes, attempts have been made to exclude it from human habitations by the removal from the vicinity of the latter of all forms of vegetation which may provide a suitable haunt for the fly. Since wild game animals act as reservoirs for some Trypanosomes it has unfortunately become necessary to reduce their numbers.

PRACTICAL WORK

Amoeba

Specimens may usually be discovered in samples of muddy water taken from the bottom of shallow ponds. Mount successive drops of the liquid on microscope slides until an amoeba is located. Watch its movements. Possibly its reaction to grains of sand, or even Algal particles, may be witnessed. The internal structure is best investigated after staining the specimens. This is done on the slide, the successive fluids being drawn from between the slide and cover-slip with blotting paper, and each new fluid introduced from the opposite side of the cover-slip. The cover-slip may with advantage be supported by two other cover-slips, placed one beneath each of two opposite edges. The drawing through is done from the other two edges. First fix (page 38) the specimens in Bouin and gently warm the slide. This operation may be done by the use of hot

fixative in a watch-glass after the culture has been stirred. 70% alcohol is then drawn through, replacing the Bouin. Replace this with iron alum, leaving for one hour. Draw through distilled water to remove the iron alum, which acts as a mordant. Stain in iron haematoxylin for one hour and then draw through tap-water. Examine under a microscope, when it will be seen that the whole of each specimen is black. Replace the stain with iron alum, examining at intervals until only the nuclei are black. Draw through tap-water. Introduce successively 30%, 50%, 70%, 90% and two lots of absolute alcohol for ten minutes each, and finally two lots of xylene for a similar period. Carefully raise the cover-slip and introduce a drop of Canada balsam. Replace the cover-slip, this time unsupported. Examine and draw.

Paramecium

A culture of *Paramecium* is readily obtained by adding hay to pond-water and leaving for some days, the hay infusion providing food for the Bacteria upon which *Paramecium* lives. Examine drops of this water for specimens. Note particularly the movement of this animal. Stain and mount as for *Amoeba*. If possible examine slides showing stages in conjugation. In making preparations it is useful to introduce a few strands of cotton-wool beneath the cover-slip, for the paramecia usually then become entangled and are less likely to be lost.

Monocystis

Make a thin smear of the contents of a portion of the vesicula seminalis of an earthworm and, *as soon as dry*, flood with fixative (90% alcohol is very suitable). Stain with haematoxylin, clear and mount. Discover and draw as many stages in the life-history as possible.

Plasmodium, Trypanosomes and Entamoebae

Examine prepared slides under oil-immersion, drawing representative specimens.

Temporary Stains

It is possible to stain specimens to show certain structures more clearly by the use of so-called temporary stains. Their use requires less well-developed technique than is the case in the making of permanent preparations. The following reagents are suitable for direct addition to a drop of culture liquid containing fresh specimens: (*a*) *Acetocarmine* – for nuclei. (*b*) *Iodine* – for cilia and flagella. (*c*) *Tannic acid* – for trichocysts. (*d*) *Dilute Indian ink* – for food-vacuoles of *Paramecium*. This last-named reagent is ingested by the animal and is therefore of value as a 'food', rather than as a stain.

CHAPTER 2

Hydra and Obelia

Both *Hydra* and *Obelia* belong to the phylum Coelenterata, the most important diagnostic feature of which is the possession of a body-cavity, bordered by a double wall and with a single opening to the exterior. In structure these two animals are very similar, but *Obelia* consists of a colony of *Hydra*-like structures communicating via a common stalk.

HYDRA

Although there are several species of *Hydra*, based partly on colour and partly on other factors, the following generalised description may be taken as applicable to all of them. Thus *Hydra viridis*, known also as *Chlorohydra viridissima*, is green (see later), *Hydra fusca* is brown and has exceptionally long tentacles, whereas *Hydra attenuata*, also brown, has much shorter tentacles.

Structure

Hydra lives in fresh water, chiefly in ponds and ditches, where it is found attached by a discoid, adhesive base, termed the **foot**, to a substratum of water-weeds. It is visible to the naked eye, and may be found in either an expanded or a contracted condition. Its body consists of a hollow sac, bounded by two single layers of cells. These are the **ectoderm** on the outside, and the **endoderm** bordering the **coelenteron**. This latter communicates with the exterior by a **mouth**, situated at the free extremity of the animal on a projecting **hypostome**, and surrounded by a ring of some eight **tentacles**. These are formed as evaginations, or finger-like out-growths. of the body-wall of the animal, and are therefore two layered. Into each the coelenteron extends for some distance. Separating the two layers of the body-wall is a gelatinous **mesogloea**. It is frequently possible to distinguish a small, lateral bud on such an individual, resembling the parent form in all but size. Not far behind the tentacles in a mature individual there may appear thickenings of the body-wall, visible as small lobes on the ectoderm. These are the **testes**. Nearer to the foot is a similar but larger structure. This is an **ovary**, within which a single egg-cell, or ovum, ripens. The structure of the layers of the body-wall is extremely important on account of the fact that the cells comprising them have become differentiated – *i.e.* modified to fulfil special purposes. The types of cell concerned are described below, where the two layers of the body-wall are considered in detail.

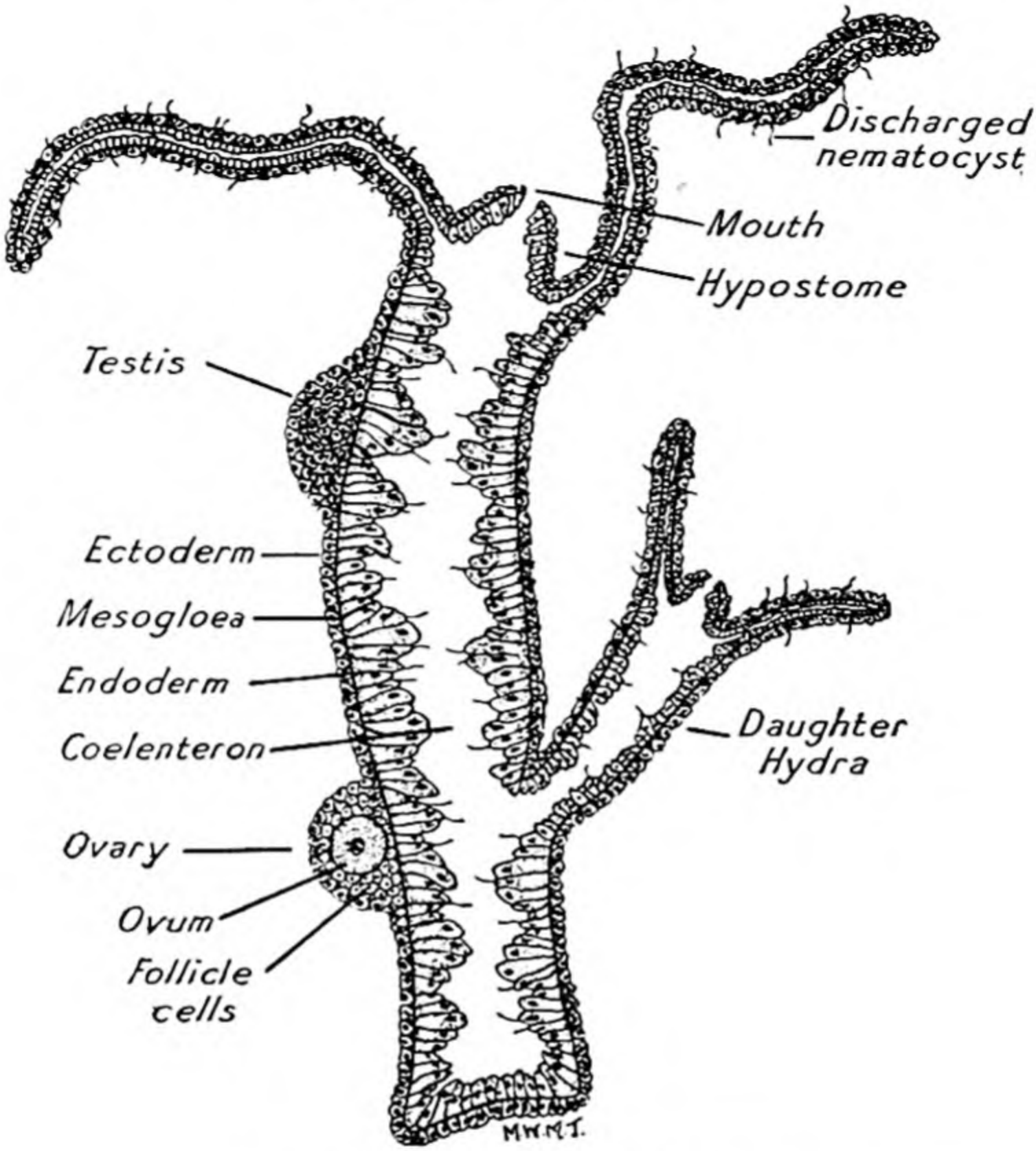


FIG. 12 – *Hydra*. Longitudinal section.
(For convenience gonads and bud are shown on the same individual.)

ECTODERM. The ectoderm is mainly composed of two types of cell, namely the **musculo-epithelial** cells and the **interstitial** cells. The former are vacuolated and are widest at their outer end, tapering towards the base, which is itself expanded in a plane parallel to the longitudinal axis of the animal. The expanded plates of all the musculo-epithelial cells constitute a more or less continuous lining within the superficial layers of the body, and exhibit considerable powers of contraction, so that the body as a whole can be considerably reduced in length, whilst a certain degree of locomotion of this normally sessile organism can be effected.

The effect of the tapering of the epithelial portions of these specialised ectodermal cells towards their inner ends must be to introduce spaces

between them. These spaces are occupied by small groups of undifferentiated cells, known as **interstitial** cells. These retain the power of division and are responsible for the origin of new ectodermal cells of the modified types. Embedded at intervals in the ectoderm layer are highly specialised cells, termed **nematoblasts**. These are especially numerous on the

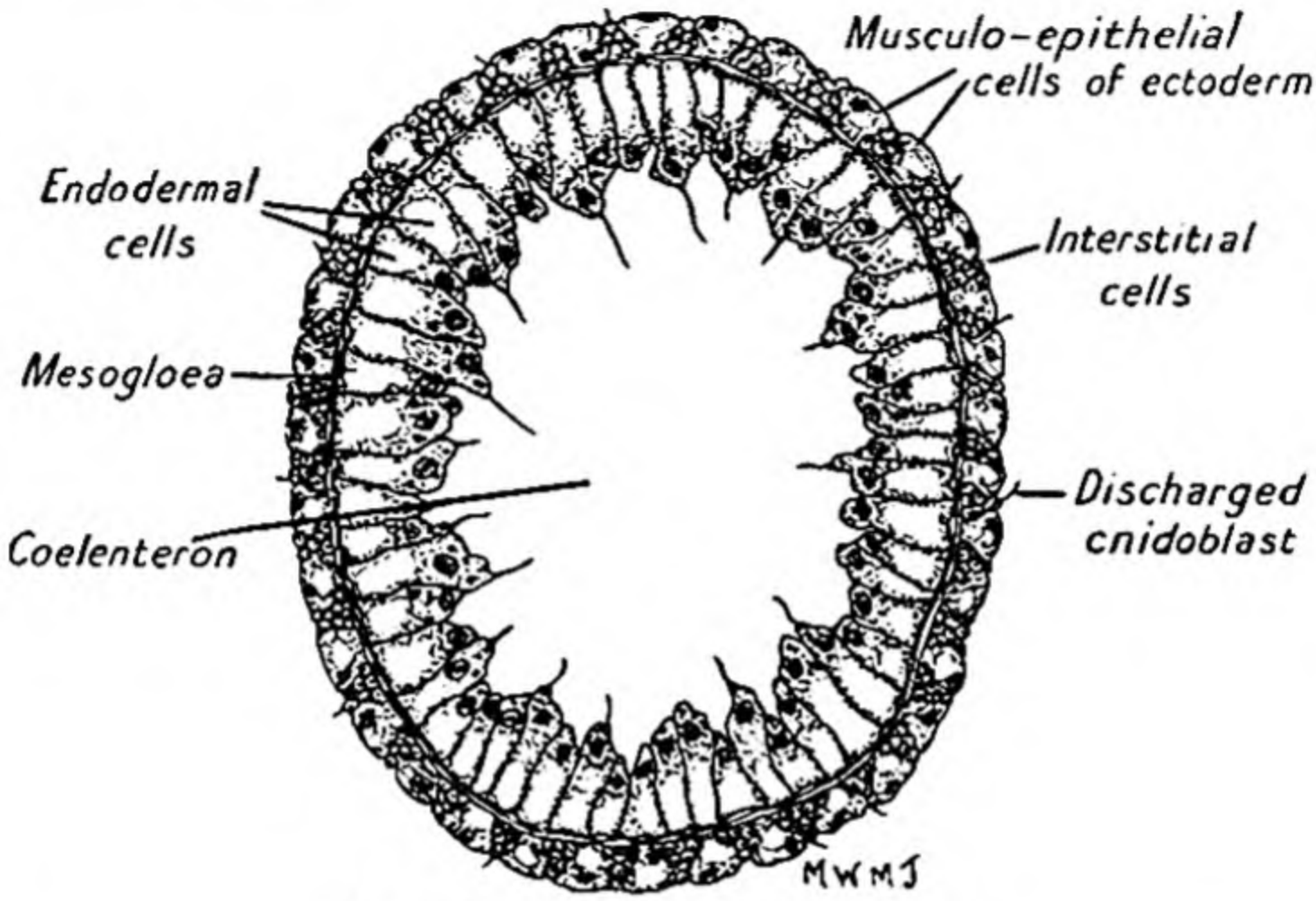


FIG. 13 – *Hydra*. Transverse section.

tentacles and to a lesser extent occur just below the hypostome. They are of four distinct types, of which the largest and most complex are the *penetrants*, so called on account of their function of piercing and paralysing the animal's prey. Each consists of a hollow cell, the aperture leading to the exterior being closed by a hinged lid, or *operculum*, whilst the lining of the cavity bears a ring of small, rod-like bodies, to each of which is attached a contractile fibre. Within the cavity, which is fluid-filled, is a peculiar, thread-like, secreted body. The whole – cavity and its thread-like enclosure – constitutes the *nematocyst*. At its end nearer to the operculum the thread is wide and its lining bears three pointed stylets and a number of spined ridges. This portion is continued inwards as a long, narrow, coiled thread, as shown in Fig. 14. To one side of the operculum is to be found a short, sensitive, bristle-like *nematocil*, contact with which may trigger off the nematocyst. It is reasonably certain that, when discharging occurs, the whole thread becomes everted, so that the stylets and spines become exposed on the outer surface of its base. The remaining types of nematoblast, although essentially resembling the penetrants, differ in respect of the form and function of their thread-like enclosures. Those of the *volvents* coil tightly upon discharge and assist in binding the prey to the tentacles by winding around any suitable

bristles. The short threads of the *small glutinants* remain straight and fulfil the same function, this time by adhesion, and also assist in locomotion (page 30). The longer threads of the *large glutinants* appear to be used as weapons of offence against small animals not used as food.

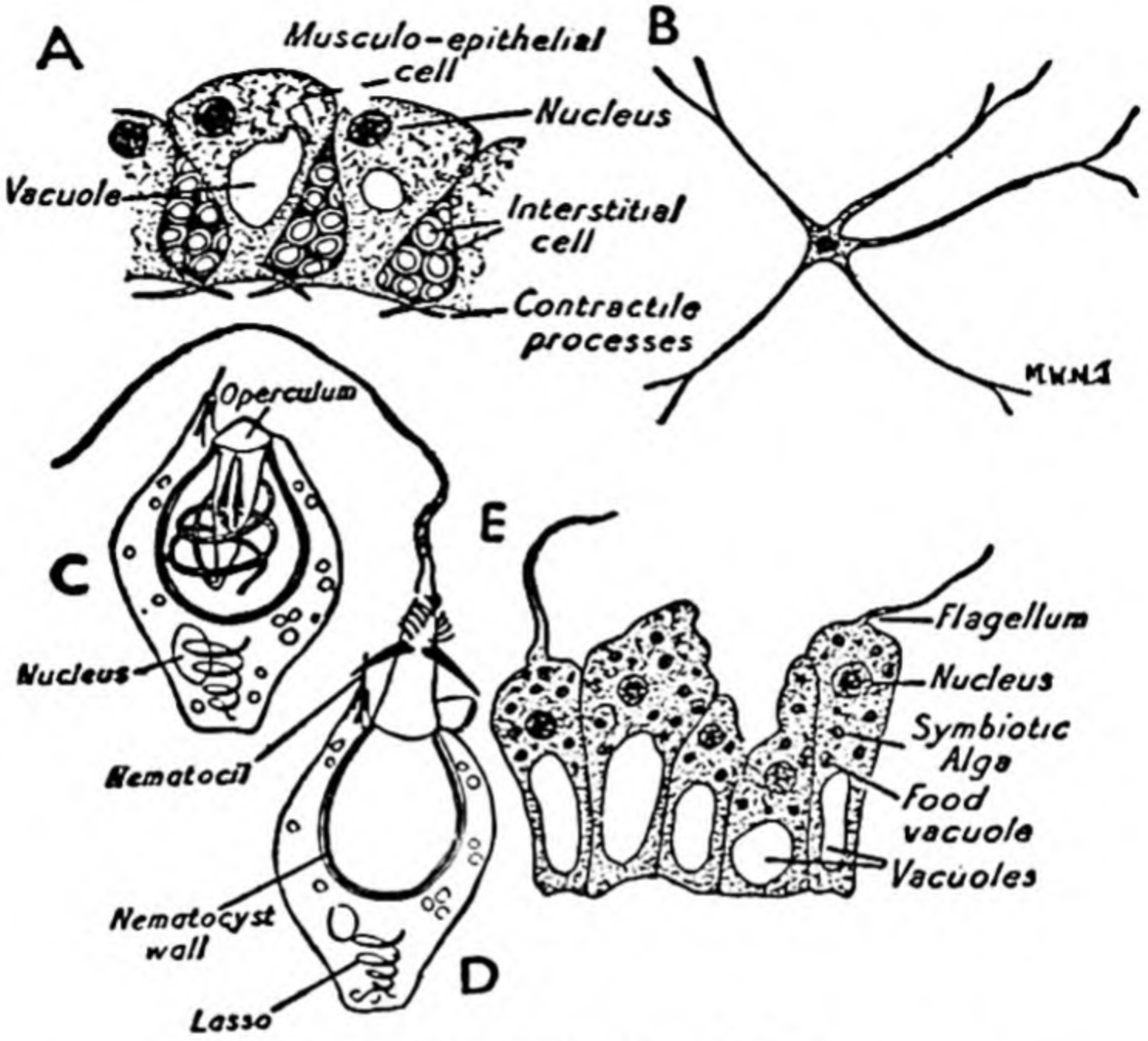


FIG. 14 – *Hydra*. Types of cell.
A., Musculo-epithelial and interstitial cells; *B*., Nerve-cell; *C*., Nematoblast; *D*., The same – discharged; *E*., Endoderm cells. (*C* and *D* – After Baker.)

The position of the nematoblasts almost exclusively on the tentacles is especially peculiar in view of the site of their origin. Arising from interstitial cells in the ectoderm of the middle third of the body, young nematoblasts migrate through the mesogloea into the endoderm. Ultimately they are discharged into the coelenteron, either naked or enclosed within an endoderm cell. Many find their way into the hollow tentacles, where they are ingested by the pseudopodia of some of the endoderm cells, ultimately to reach the tentacular ectoderm, where they complete differentiation.

Sensory cells occur at intervals amongst the musculo-epithelial cells, which they may actually penetrate. Superficially each bears a minute, conical projection, extending beyond the surface, whilst its base is con-

tinued as a delicate, conducting fibre, contiguous with the nerve cells of the mesogloea (see below).

Gland cells are abundant in the foot, where they secrete the adhesive substance attaching the animal to the substratum. Other gland cells in the vicinity of the hypostome secrete mucus which may facilitate the passage of prey into the mouth.

Nerve cells are embedded in the mesogloea, although they are of ectodermal origin. Every cell is composed of a cell-body, containing the nucleus and bearing a series of branching fibres, those of adjacent cells forming synapses (page 462), so that an impulse-conducting network is present throughout the whole mesogloea. Some branches terminate in the bases of musculo-epithelial cells, which they may stimulate, whilst others are in close connexion with the fibres of the sensory cells.

Finally it should be noted that the interstitial cells also give rise to the gonads and their contained germ-cells. These organs are described on page 32.

ENDODERM. The endoderm cells are of much more uniform structure. They are cylindrical in shape, but the majority of them are subdivided at the ends bordering the coelenteron, some possessing the power to form pseudopodia, as in *Amoeba*, whilst others bear delicate flagella. In the region of the mouth and tentacles the cells are more regular in outline and are glandular. The bases of all these cells are expanded into contractile processes, but these extend transversely around the body, and not longitudinally, as do those of the musculo-epithelial cells. The cells, in the *viridis* species, are vacuolated and frequently contain numerous Algae, belonging to the groups Zoochlorellae and Zooxanthellae. The pigments (chlorophylls) which these plants contain impart the characteristic green colour to the *viridis* species. The significance of these algal inclusions is discussed on page 679.

Physiology

Apart from its restricted powers of locomotion and, in the case of *Hydra viridis*, the augmented source of food materials, *Hydra* exhibits the usual types of physiological activity essential to life.

NUTRITION. *Hydra* feeds upon water-fleas (*Daphnia*) and other small water animals. The marked motility of its prey is interesting in view of the animal's own sessile habit. The prey is captured and manipulated by the tentacles. Contact with the nematocils is responsible for the discharge of the nematocyst threads, the functions of which have already been described (page 27). All the tentacles combine to convey the captured prey to the mouth, which has already opened widely in response to the diffusion of *glutathione* from the ruptured tissues of the victim. Once inside, the mouth closes and churning movements produced by the contraction of the body-wall muscles result in fragmentation of the food. Some digestion occurs in the coelenteron, aided by the alkaline juice

liberated by the gland-cells of the endoderm, and the soluble products of digestion are absorbed. The smallest particles are ingested by the pseudopodia of the endoderm cells and undergo intra-cellular digestion in the food vacuoles. Nerve-cells and cells of the outer ectoderm receive their food-supply by simple diffusion through the mesogloea. Undigested remains of the small ingested particles are reconveyed to the coelenteron, possibly wafted forwards by the flagella, and certainly discharged through the mouth, together with such matter as has never entered the endoderm cells – *e.g.* the exo-skeleton of a water-flea.

RESPIRATION. Gaseous exchange is effected exclusively by simple diffusion. But it must be borne in mind that the surface-area of *Hydra* is appreciable, especially on account of the possession of long, slender tentacles, whilst fresh water is frequently taken into the coelenteron, so that the endoderm layer can then act as a respiratory surface. Furthermore, the animal's attached mode of life severely limits its oxygen requirements.

OSMO-REGULATION. It has been suggested that there may exist a higher osmotic pressure (page 377) in the nematoblasts than in other body cells, thus causing water to accumulate in the former. Upon discharge of nematoblasts such water would be eliminated. This mechanism alone, however, could hardly operate on a sufficiently large scale to be completely effective.

EXCRETION. This again is by simple diffusion, from the ectoderm cells directly into the surrounding water and from the endoderm layer into the coelenteron.

LOCOMOTION. In addition to the ability to flex itself and its tentacles, a certain degree of locomotion is possible to this normally sessile organism. This is effected by 'looping' or 'somersaulting'. In both cases the body first elongates and then bends over for the tentacles to become attached to the substratum by means of the small glutinants. The foot is then released and may be either drawn up nearer to the tentacles or swung right over to the other side. In either event the foot is re-attached and the tentacles released. Occasionally a hydra floats at the surface by virtue of the secretion of a bubble of gas at the centre of the foot, becoming re-attached when the gas disperses.

IRRITABILITY. The branching nerve-cells, by reason of the contiguity of their processes, establish a nerve net in the mesogloea. Applied stimuli appear to generate impulses which travel with equal facility in all directions from the point of contact. These impulses appear to fade out with increase of distance from that point. This can be explained on the grounds that some of the early impulses, whilst failing to bridge the synaptic gaps between adjacent fibres, may lower the resistance to succeeding impulses. This phenomenon is termed inter-neural facilitation. Thus the farther away from the point of contact the impulses have to travel the less of them will get through. All such stimuli as create impulses

for transmission through the nerve net are perceived by the sensory cells, Although there is no rudiment of co-ordination in this primitive system, special through-conduction paths exist. Thus, if *Hydra* be strongly stimulated, as by vigorous disturbance of the water in which it is living, impulses are conveyed rapidly to all parts, resulting in the extensive contraction of both the body and the tentacles. All species of *Hydra* show a marked tendency to seek a well-illuminated environment.

The nematoblasts are described as independent effectors – *i.e.* they respond directly to contact with the nematocils and are not controlled through the nerve net. But to some extent their response is conditioned. Thus the small glutinants respond readily to sustained light-weight stimulation. This is manifestly in adaptation to their function in providing temporary attachment during locomotion. The penetrants and the volvents respond to harsher stimulation, but only in the presence of juices normally exuding from such animals as *Hydra* preys upon. Thus they are rarely wasted in attacks upon bodies unsuitable as food.

Life-history

There are two seasonally-determined phases in the life-history of *Hydra*. In favourable conditions a considerable number of daughter individuals may be formed from a single parent by the asexual process of budding. At a point usually in the lower half of the animal both layers become evaginated, so that there is formed a hollow bud, into which

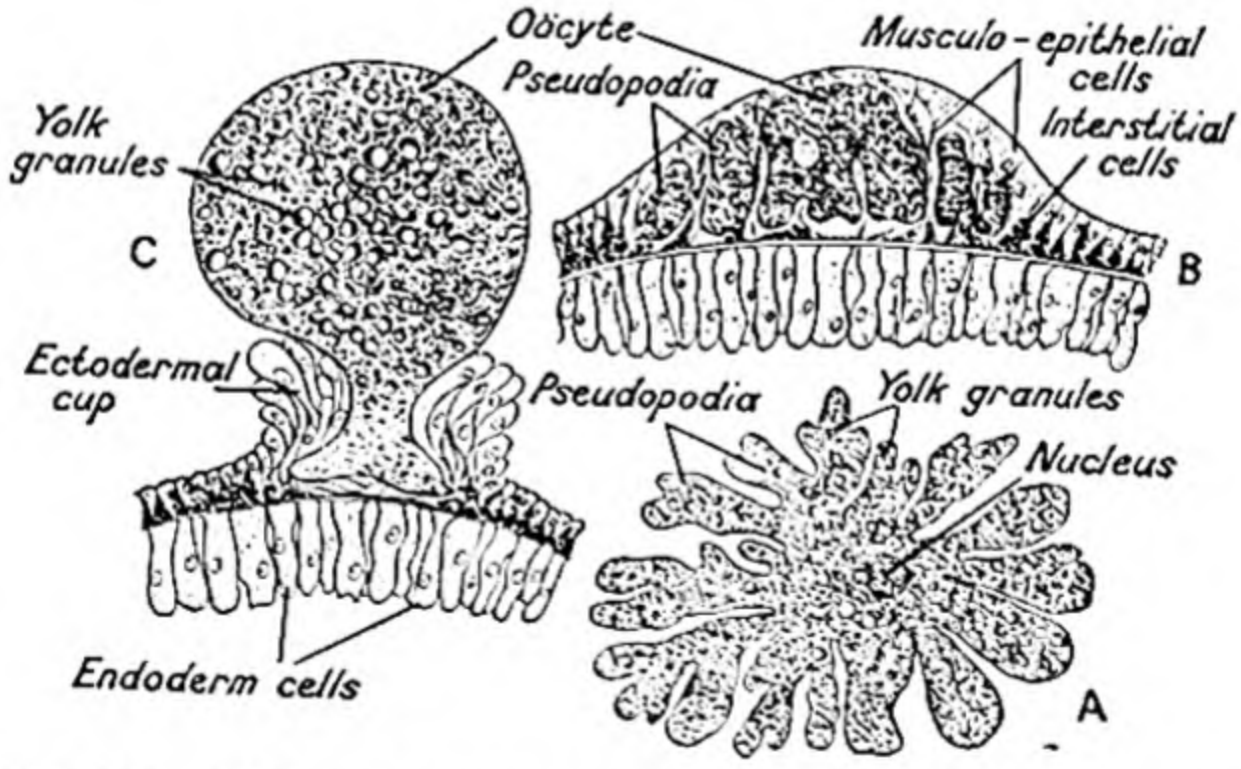


FIG. 15 – *Hydra*. An ovary. *A*, A maturing oöcyte, showing amoeboid structure; *B*, Section of an ovary, distending adjacent musculo-epithelial cells. The oöcyte has grown at the expense of a large number of interstitial cells, some of which can be seen. Being amoeboid, the sectioned oöcyte often appears as small, disconnected fragments, as indicated; *C*, A fully mature oöcyte, seen sectionally in situ; it remains rooted at its base until after fertilisation and completion of the early stages of development.

extends the coelenteron. The bud is originated as a result of the evagination of the body-wall of the parent. By a number of similar evaginations at the distal end of the bud tentacles are formed, whilst in the midst of these a mouth is perforated. Several buds may be formed simultaneously upon the same parent, and it is even possible for secondary buds to be produced on an original one before the latter is separated from its parent. Liberation is eventually effected by a constriction of the base of the bud, which, after being set free, soon attaches itself to a water-weed or other suitable object. Occasionally *Hydra* may reproduce asexually by a division of the whole body, either transversely or longitudinally, into two parts, each of which must develop new structures. Akin to the process of asexual reproduction is the power of *Hydra* to effect regeneration. If a single individual be cut into pieces, any portion not less in size than a certain quite small minimum will grow into a complete animal.

The sexual phase in the life-history of *Hydra* results in the production of a resistant body, and hence is primarily of survival value. The ovaries and testes originate by the rapid multiplication of interstitial cells. In the ovary one of these cells soon becomes noticeably larger than the remainder, extending pseudopodia wherewith it engulfs the surrounding cells. In this way it acquires a supply of reserve food and ripens to form a mature ovum. Eventually it bursts through the superficial layer of cells covering it to become exposed on the surface of the animal. The testes

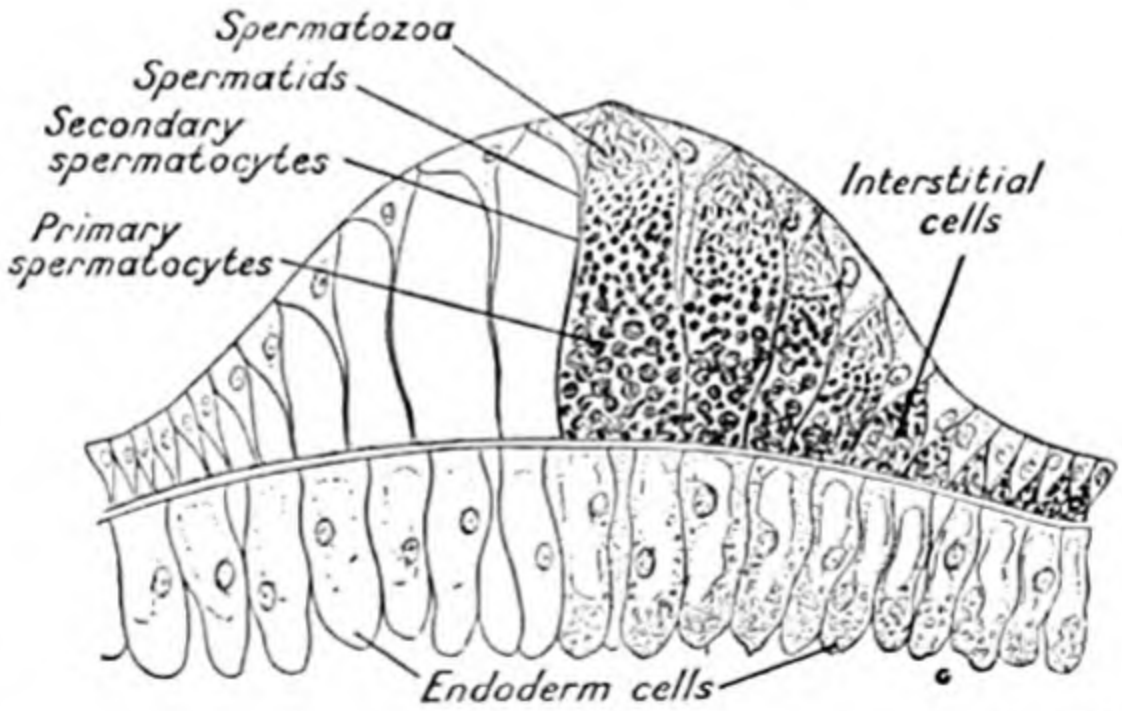


FIG. 16 – *Hydra*. Section through a mature testis. The stages in maturation of the spermatozoa are comparable with those in vertebrates, described on page 318. When the testis bursts the mature spermatozoa are released.

arise as a series of swellings near the distal end. Within each testis very many spermatozoa are formed, and these are presently shed into the water. Fertilisation is effected by the penetration of an egg by a spermatozoön to form a zygote. Since the testes ripen before the ovary on any

given individual cross-fertilisation is practically assured. This zygote undergoes division, and eventually a hollow ball of cells, bordered by a single wall and known as a **blastula**, is formed, the cavity of which is termed a **blastocoel**. Into this blastocoel migrate cells, formed by division of the cells of the single wall, and in this way a double-walled sphere is produced. These two layers eventually constitute ectoderm and endoderm respectively, though at this time so many cells are proliferated from the ectoderm that the endoderm becomes a solid ball. The ectoderm

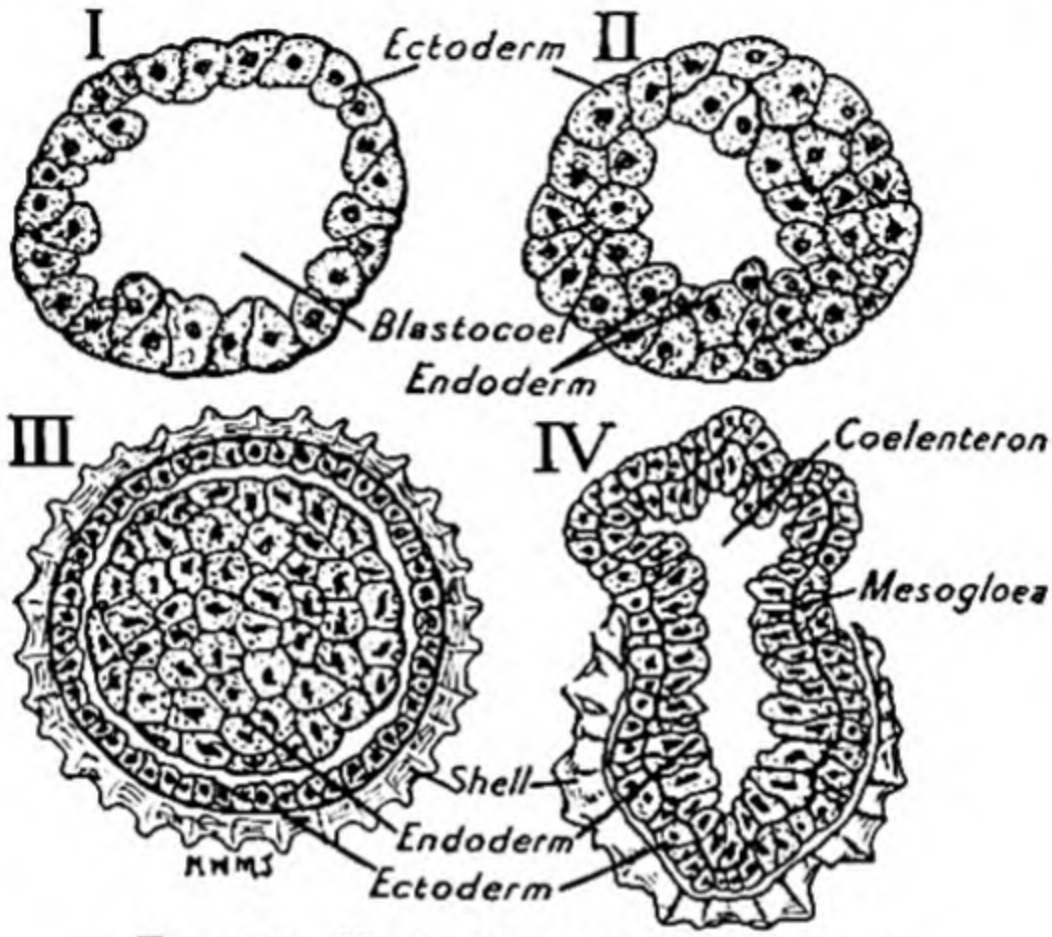


FIG. 17 – *Hydra*. Stages in development.

now secretes a horny capsule about itself, and the embryo drops away from the parent hydra or is attached to the substratum. Within this shell a period of rest ensues, and this stage affords an efficient resistance against adverse conditions. The capsule subsequently bursts and the embryo emerges. A split occurs in the midst of the endoderm, thus giving rise to a coelenteron. Finally a mouth is perforated, whilst tentacles are evaginated. Attachment quickly follows and thus the process of development is completed.

OBELIA

Obelia, which is found living attached to sea-weed near low water mark, is a colony of *Hydra*-like components, and in structure it may be compared with *Hydra* which has undergone repeated budding, but the buds have not become separated from the parent.

Structure

The budding above referred to must be visualised as having taken place regularly, so that there is produced an orderly arrangement of

polyps, as the separate *Hydra*-like structures are called, on a common stalk, termed the **hydrocaulus**, the base of which is branched, forming the **hydrorhiza**, serving for attachment to the substratum. Hydrocaulus and hydrorhiza together constitute the **coenosarc**. These polyps are of two kinds, known respectively as **hydranths** and **blastostyles**. The hydranths are comparatively numerous, and each closely resembles *Hydra* in appearance. It is distinguishable from *Hydra* by the fact that the tentacles are solid, being filled with large, endoderm cells, and there

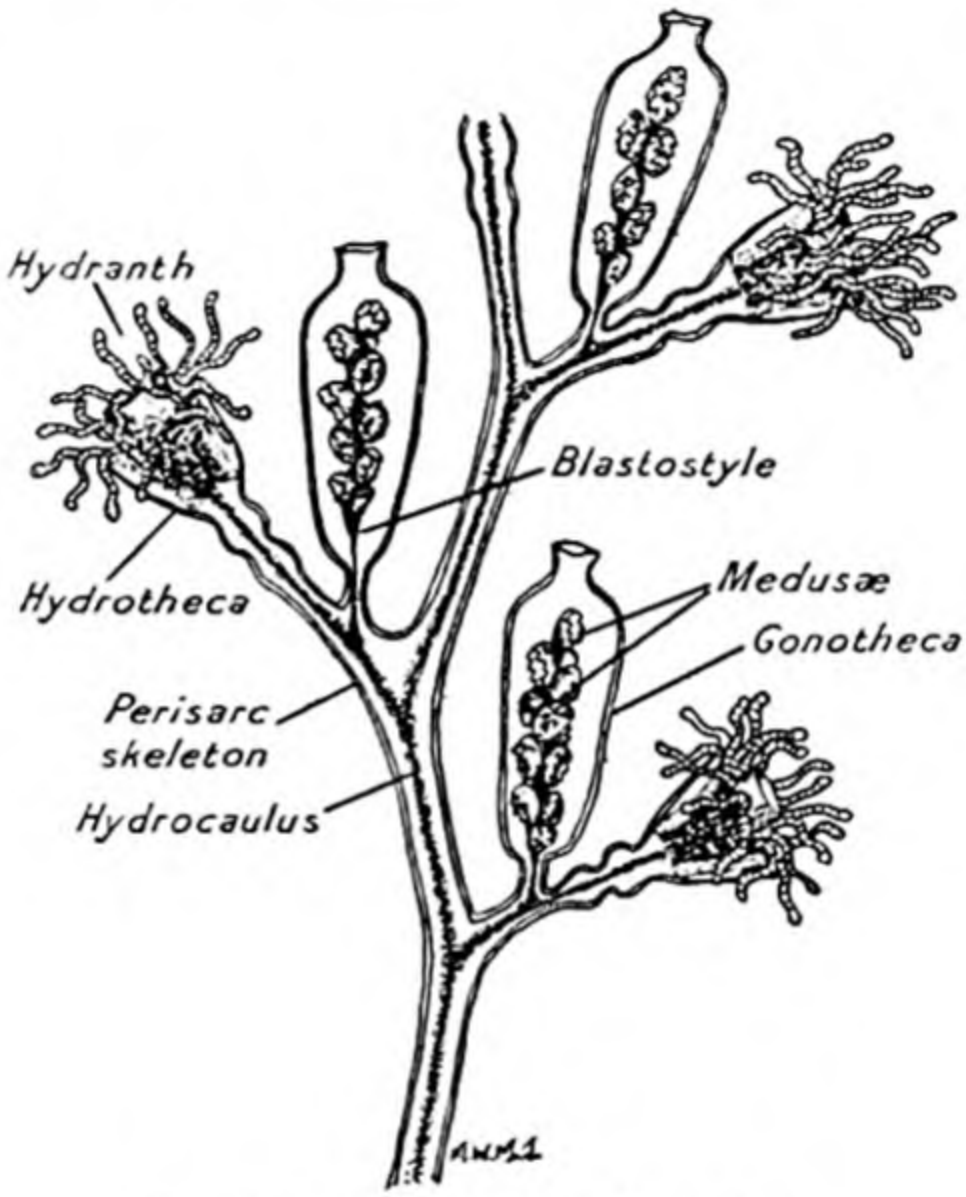


FIG. 18 – *Obelia*. Part of a colony.

are more of them than in *Hydra*. The coelenteron itself is slightly modified, for, just within the mouth, this cavity in the relatively large hypostome has become expanded, leading via a constricted aperture into the coelenteron proper. Instead of being fixed to the substratum as in *Hydra*, the base of the hydranth remains open, its coelenteron communicating with the cavity of the hydrocaulus, passing as it does so through the narrow stalk by which each hydranth is attached to this principal axis. The ectoderm cells of *Obelia* are different from those of *Hydra* in one important respect. Whereas *Hydra* possesses musculo-epithelial cells, these two portions have become segregated in *Obelia*, so that a continuous muscular coat lies within, and separate from, a superficial epithelium. Interstitial cells are virtually absent and nematoblasts, arising in the ectoderm of hydranths and coenosarc, migrate to the

tentacles, where differentiation of the nematocysts is completed.

Blastostyles appear only when the colony has reached a considerable size. Each occurs in the axil between the hydrocaulus and the stalk of a hydranth. Superficially it is easily distinguishable from a hydranth, though the two are fundamentally similar structures. It has no mouth or tentacles, whilst the coelenteron is severely restricted.

The whole colony is invested in a horny case, or **perisarc**, secreted by the ectoderm, and slightly separated from the outline of the animal. The perisarc is expanded into an open, cup-like structure, known as a **hydrotheca**, to enclose each hydranth, and into a similar **gonotheca**, to enclose each blastostyle. The mouth and tentacles of the hydranth normally project from the hydrotheca, but can be withdrawn if necessary. Every hydrotheca stalk bears two or three annular constrictions, whilst in the lining of the base of every hydrotheca itself is a circular ridge which supports the hydranth.

The hydranths are the nutritive members of the colony, and the food which they absorb is distributed through the hydrocaulus to one another and to the blastostyles, whose function it is to bud off a modified form of polyp, known as a **medusa**.

Medusa

By evagination of ectoderm and endoderm of a blastostyle medusae are formed, and these eventually become detached to escape from the colony via the mouth of the gonotheca. A medusa is typically umbrella-shaped, the convex surface being known as the **ex-umbrella**, the concave surface as the **sub-umbrella**, whilst the short, handle-like structure is

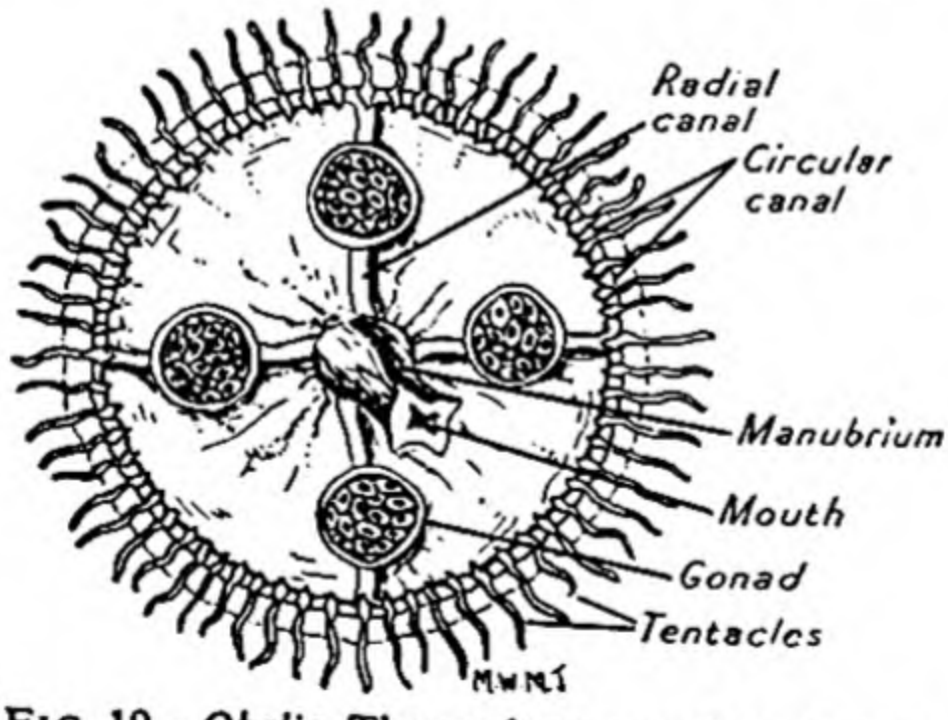


FIG. 19 – *Obelia.* The medusa, seen from below.

termed the **manubrium**. Around the margin of the medusa and projecting inwards is the **velum**, whilst the outer edge is fringed with tentacles. The tip of the manubrium surrounds the mouth, leading through the gullet, which is the cavity of the manubrium, into a stomach, situated in the

middle of the body at the base of the manubrium. From this structure four **radial canals** lead into a **ring-canal** around the margin of the umbrella. Well-developed muscle fibres lie just within the sub-umbrellar ectoderm, whilst around the rim of the medusa occur two **nerve-rings**, the larger, ex-umbrellar ring supplying the tentacles and the smaller, sub-umbrellar ring the musculature. Within the entire sub-umbrellar surface is a nervous network. With the development of these nerve-rings the initial stages of nervous co-ordination are witnessed, as is seen to a slight degree in the locomotion of *Hydra*, though, as will be remembered, in *Hydra* the

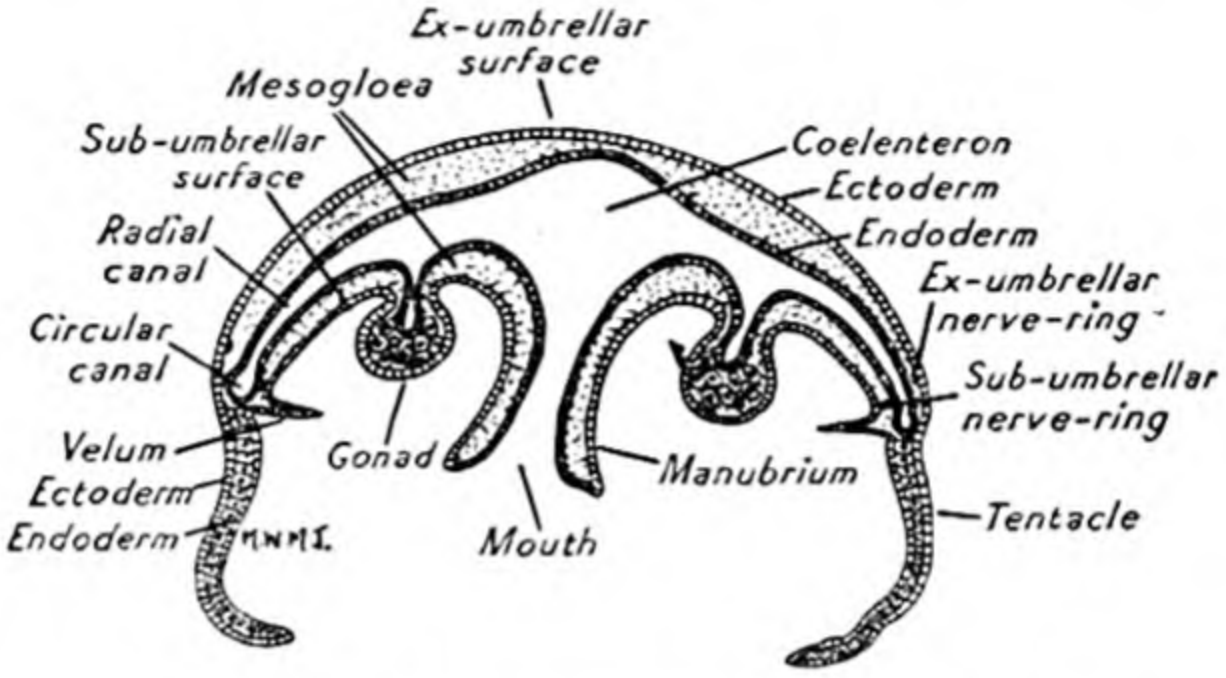


FIG. 20 – *Obelia*. Vertical section of the medusa.

nerve-cells constitute a network, with no apparent mechanism of centralisation exhibited. Changes in orientation are perceived by means of eight equally spaced **statocysts**. Each statocyst occurs at the base of a tentacle and consists of an ectodermal sac, containing a particle of calcium carbonate, known as a statolith and secreted by a single cell. The wall of the statocyst is sensitive on the marginal side, and a bunch of sensitive processes arches over the statolith. Changes in orientation modify the positions of the statoliths, resulting in the conveyance of impulses to the nerve-ring, so that equilibrium may be re-established.

It would appear at first sight that a medusa is quite unlike a hydranth in structure. But if it be imagined that the manubrium corresponds to the hypostome of the hydranth, then, if the hydranth were longitudinally compressed and transversely expanded, a structure very like a medusa would be formed, assuming that the coelenteron were obliterated save for four radial canals, joined around the margin of the disc.

But the principal significance of the medusa is that it affords a means of distribution, mainly through ocean currents, and also that it reproduces sexually. Locomotion is effected by a contraction of the muscles of the sub-umbrellar surface, so that water is driven out and the organism propelled ex-umbrellar surface first. The sexes of the medusae are

separate, each giving rise to either spermatozoa or ova, but not both. The germ mother-cells, from which the gametes are formed, originate in the ectoderm of the blastostyles, subsequently migrating to the medusae. They come to rest in the ectoderm of the latter on the sub-umbrellar surface, where they develop into gonads, either ovaries or testes. Thus there is one gonad on each radial canal. On reaching maturity the walls of the gonads burst, and both eggs and sperms are shed into the surrounding water, where fertilisation of an egg by a sperm results in the production of a zygote. Development of this proceeds in much the same way as in *Hydra*. By cleavage (division of the egg, with the products remaining attached) a hollow **blastula** is formed, the cavity of which becomes obliterated by the invasion of cells from the bordering wall to form a solid mass of endoderm. Later a split appears in this, but instead of now secreting a horny case and undergoing a period of rest, as does *Hydra*, the ectoderm becomes ciliated and a larva, known as a **Planula**, is formed, which swims about for some time. Subsequently a split appears in the endoderm and attachment by one end of the larva is effected, whilst the other becomes perforated to form a mouth, around which tentacles appear. The polyp thus produced commences to bud in a regular manner, and in this way a new colony is formed.

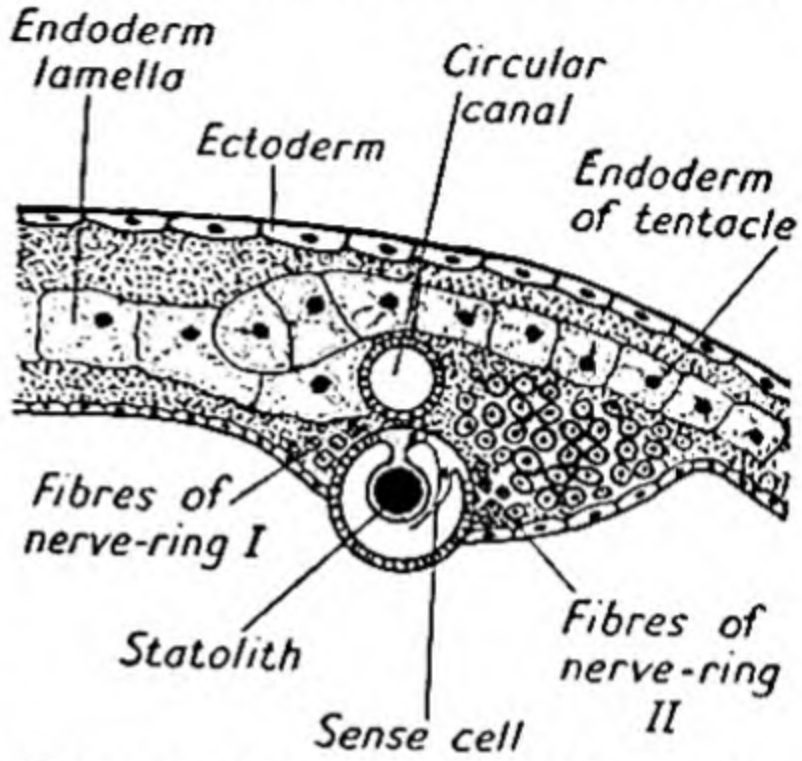


FIG. 21 – *Obelia*. Longitudinal section of the base of a tentacle, passing through a statocyst. (After Grove and Newell.)

Two phenomena of general biological significance arise from a study of the structure and life-history of *Hydra* and *Obelia*. They are individuality and alternation of generations, and are discussed in Chapters 21 and 32 respectively, where these topics are under consideration with reference to animals and plants collectively. Various modifications of the hydroid form of the Coelenterata are noted in Chapter 37, which deals with classification.

PRACTICAL WORK

Hydra is abundant in ponds, ditches and slow-running streams. It is visible to the naked eye, and therefore staining operations may be carried out in a watch-glass. Alternatively they may be effected on a slide, necessary fluids being introduced and removed by means of a fine-pointed pipette.

Place a single hydra in a watch-glass and add to it a mercuric acetic

solution (see Appendix). This fixes the organism, killing it and rendering it more or less stable in chemical form. After half an hour the fixative is removed (if using a pipette take care, since mercuric acetic is poisonous!) and replaced by 70% alcohol, containing an excess of iodine. Draw this off almost at once and add borax carmine. Leave the specimen in this for an hour and then return it to 70% alcohol. Examine under the microscope, and if over-stained leave in the alcohol until sufficient of the stain has dissolved out. Replace the 70% alcohol first by 90%, then by two successive lots of absolute alcohol and finally by xylene, allowing about five minutes for each. Transfer to a slide, cover with fairly thin Canada balsam and place a cover-slip in position. Examine carefully and draw.

Examine and draw transverse and longitudinal sections of *Hydra*. Draw small portions of each layer under high power so as to show details of cellular differentiation.

Mount *Hydra* in 1% salt solution. Place over it a cover-slip. Tap the latter sharply, when the nematocysts will be seen to explode and discharge their threads.

Obelia is found attached to the fronds of sea-weed, and a permanent preparation may be made as for *Hydra*.

Examine very carefully and draw a whole Obelia colony, a single hydranth, a blastostyle and a medusa.

CHAPTER 3

Fasciola and Taenia

Fasciola, known popularly as the Liver Fluke, and *Taenia* – the Tape-worm – belong to the phylum Platyhelminthes. Members of this phylum differ from those of the Coelenterata in that their bodies are clearly divisible into three cellular layers, and from higher animals in that they have no secondary body-cavity, or coelom and no blood system. Many of them are parasites, though free-living forms exist – *e.g. Planaria*. The two members of this phylum to be described are both parasitic.

FASCIOLA

Fasciola is frequently found inhabiting the bile-duct of sheep fed in damp meadows.

External Characters and Body-wall

In appearance it is a brown, flat worm, about an inch in length and half an inch wide. At the front end is a short projection, bearing the **anterior sucker**, whilst just behind this, on the under-surface, is the **ventral sucker**. In front of this latter is a hermaphrodite **genital pore**, and at the extreme posterior tip is the **excretory pore**. The whole body is covered by a **cuticle**, from which emerge short spines. Beneath this lies the **epidermis**, whose cells are sunk into an irregular network, termed the **parenchyma**, but they retain their connexion with a superficial protoplasmic layer, within which lie circular and longitudinal muscles.

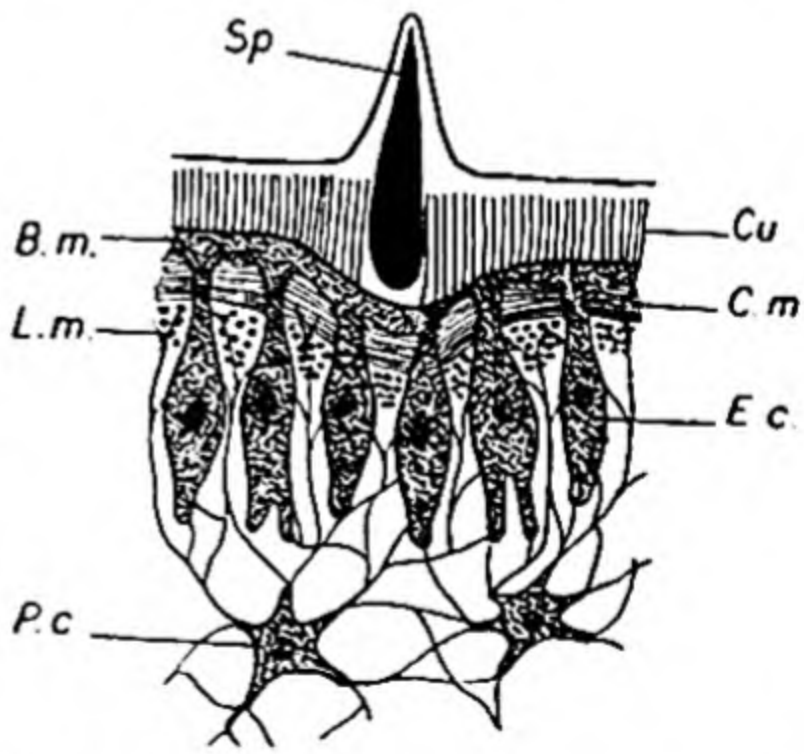


FIG. 22 – *Fasciola*. Vertical section of the body-wall. (After Saunders.)
B.m., Basement membrane; *C.m.*, Circular muscle; *Cu.*, Cuticle; *E.c.*, Ectoderm cell; *L.m.*, Longitudinal muscle; *P.c.*, Parenchyma cell; *Sp.*, Spine.

Internal Structure

Surrounded by the anterior sucker is the mouth, which leads into a muscular **pharynx**. This bifurcates almost immediately,

the two branches running to the extreme posterior end. During its passage backwards each limb of the gut gives off a large number of blind, branched diverticula. There is no opening to the exterior other than the mouth. The food consists mainly of blood absorbed from the host.

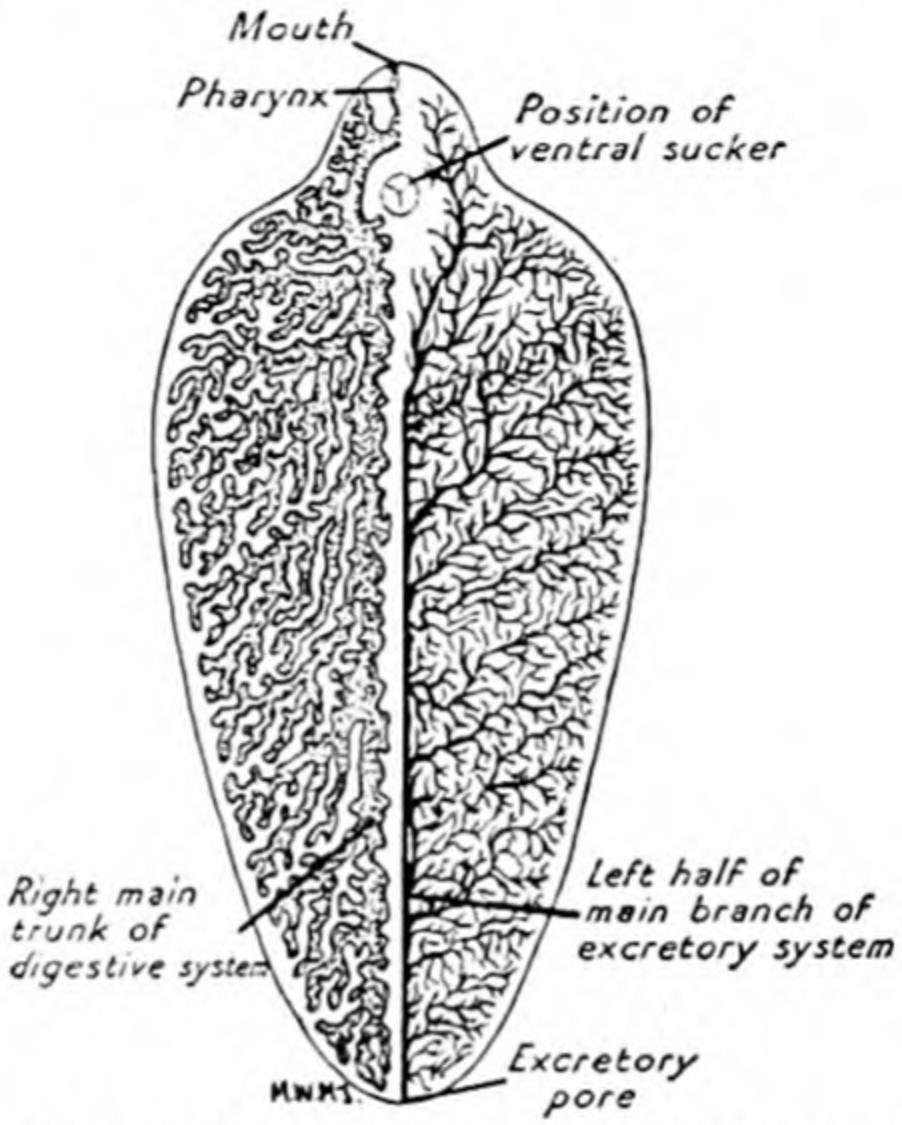


FIG. 23 – *Fasciola*. Excretory and alimentary systems. Only one half of each system is shown.

In the middle line of the body, running in the parenchyma, is a longitudinal duct, opening to the exterior via the excretory pore, from which it passes forwards for about two-thirds of the length of the animal. It is very much branched on either side, and each branch terminates in the form of a **flame-cell**. A flame-cell may be compared with a hollow pin, with a bunch of cilia hanging into the cavity from the upper (head) end. These, by their lashing movement, keep the contents of the cavity in motion, thus preventing the accumulation of a layer of concentrated solution near the lining of the flame-cell.

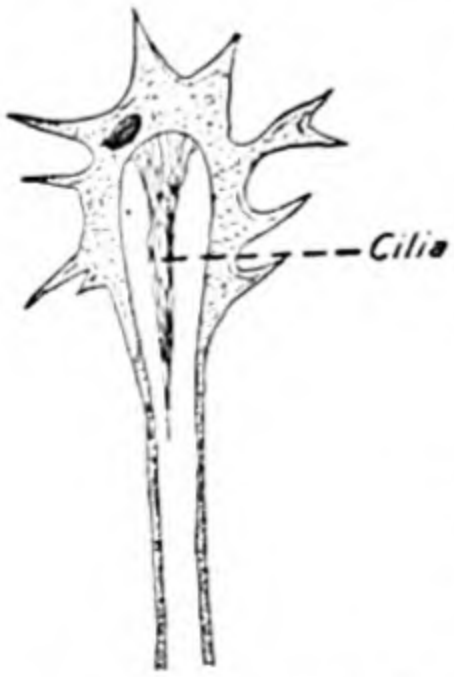


FIG. 24 – Flame-cell.

In the region of the pharynx are two **cerebral ganglia**, joined dorsally by a **commissure**. From these ganglia three pairs of nerves run longitudinally to the hind end of the body, giving off branches on their course. They are connected at intervals by transverse hoops.

Fasciola is a hermaphrodite – *i.e.* every

individual bears both male and female reproductive organs. There is a pair of branching **testes**, one lying anterior to the other. Sperms from both are collected up into a **vesicula seminalis**, where they are stored. From this emerges a thin tube, somewhat modified at its free end to form a muscular **penis** (or cirrus). This normally lies invaginated within a **cirrus sac**, but it can be evaginated to be thrust out of the genital pore.

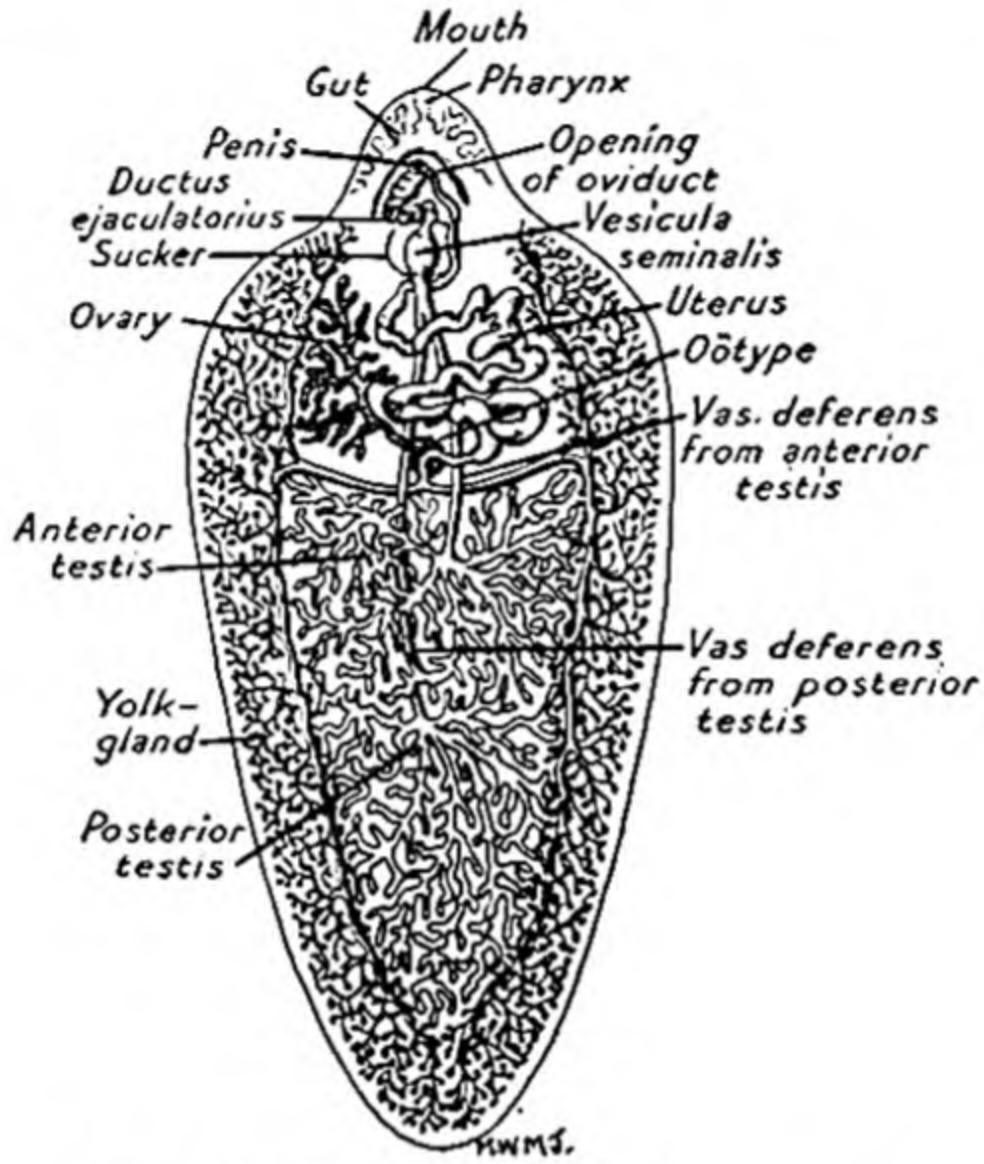


FIG. 25 – *Fasciola*. Reproductive system.

There is an unpaired, right ovary, which is itself a diffuse organ, considerably branched. From this a short, narrow tube, known as an **oviduct**, leads into a spherical chamber, termed the **oötype**, within which the eggs encounter the yolk from a pair of large and very diffuse **yolk-glands**. Each of these lies longitudinally down the sides of the body, whilst the yolk is collected into two transverse ducts, which unite in the middle line to run to the oötype. The oötype is further surrounded by **shell-glands**, and from it leads a wide, coiled tube, the **uterus**. This opens at the side of the cirrus into a common chamber, the **genital atrium**, which itself opens to the exterior by the genital pore. A minute *Laurer-Stieda* canal runs vertically to connect an aperture on the dorsal surface with the oötype. It is believed that cross-fertilisation is the rule in *Fasciola*, the penis of either member of a copulating pair being inserted into the Laurer-Stieda canal of the other. The eggs are fertilised in the base of the oviduct, yolk-cells accumulate around each and the whole becomes

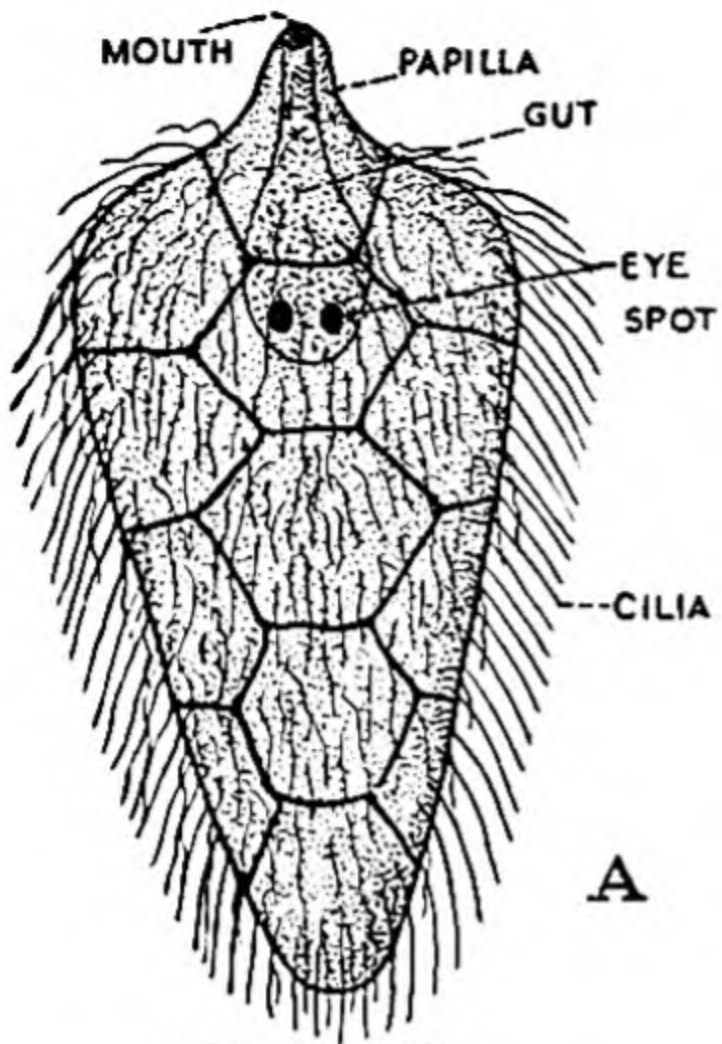
enclosed within a shell before passage forwards into the uterus, from which escape is eventually effected via the genital pore into the bile-duct of the host. The Laurer-Stieda canal may also serve for the elimination of surplus yolk-cells.

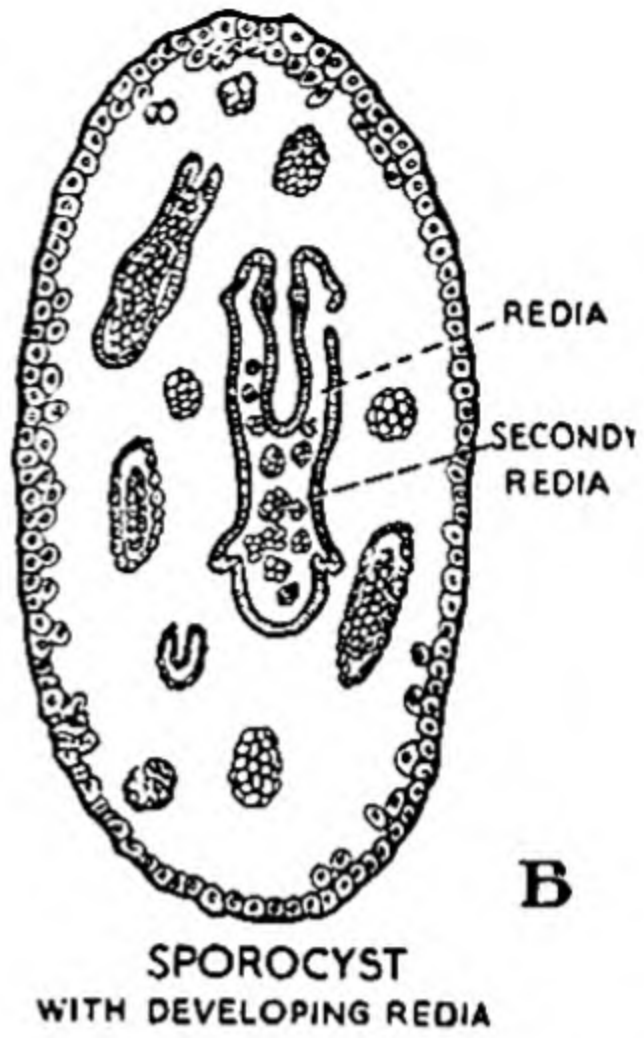
Life-history

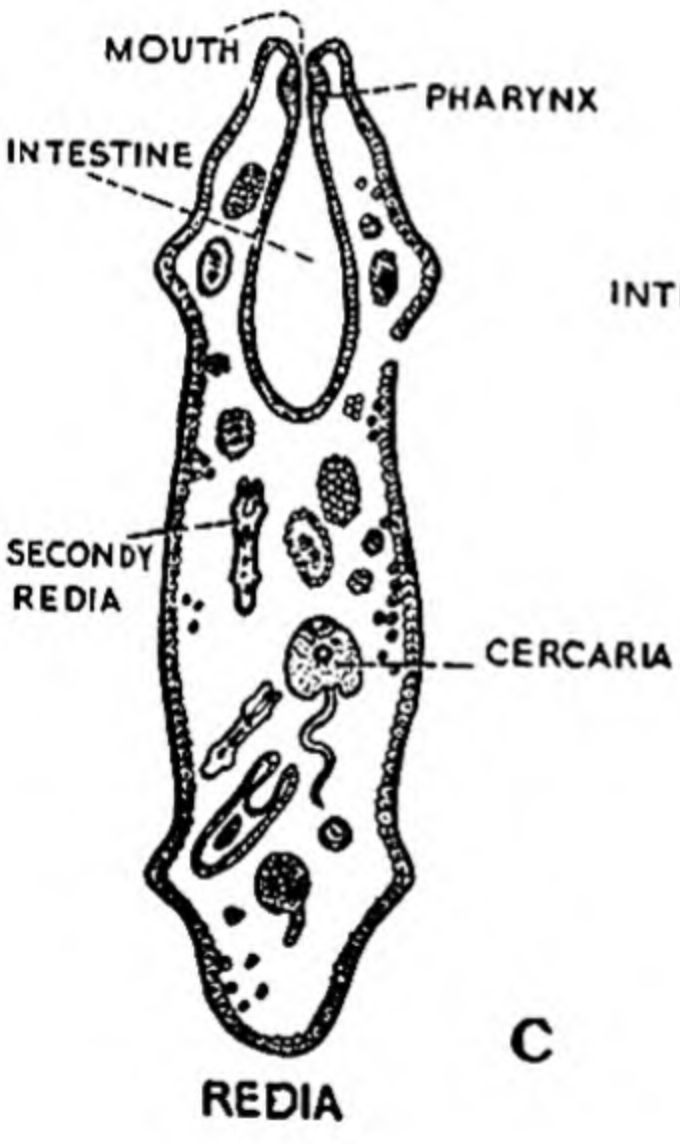
Development commences immediately after fertilisation of the eggs, each of which is divided by a first cleavage furrow into a small, granular **propagative cell**, and a large, clear **ectodermal cell**. The latter, as its name implies, gives rise to the larval ectoderm only, whilst the propagative cell divides into two, from one of which are derived the endoderm and mesoderm of the larva, and from the other the germ-cells. The developing eggs are soon passed into the intestine of the host along the bile-duct, and are eventually cast out with the faeces. Eventually a larva, known as a **miracidium**, is formed. This consists of five rows of ciliated cells (ectoderm), enclosing a blind gut and a pair of flame-cells, which communicate with the exterior. Near the anterior end are two 'eye-spots'. The bulk of the larva consists of loose, parenchymatous material, containing two groups of cells which will eventually give rise to the gametes. By means of its cilia the larva swims about until it meets a species of fresh-water snail – *Limnaea truncatula*. It then enters the pulmonary aperture of this animal, where it degenerates by the loss of its cilia and most of its internal organs to become a sac-like **sporocyst**, which contains the germ-cells of the miracidium. These develop parthenogenetically (*i.e.*, without fertilisation) into larvae, known as **rediae**. The redia is a sac-like larva, with a small mouth, suctorial pharynx and a simple gut. Towards the anterior end is an evaginated disc of ectoderm, constituting the *collar*, whilst two processes are similarly formed near the posterior end. In the case of rediae produced in the summer the contained germ-cells give rise to further generations of rediae in a similar manner. But eventually the rediae escape from the sporocyst and travel by means of the collar and posterior processes to the digestive gland of the snail. Here the germ-cells contained within the rediae give rise to a new type of larva – the **cercaria**. This possesses a heart-shaped body and rudiments of all the adult organs. The cercariae eventually pass out of the rediae in the region of the collar and move to the exterior via the pulmonary chamber of the snail. Each then secretes around itself a cyst, the product of cells lying just below the surface. Each encystment generally occurs in water, and survival is possible for up to a year. Only when the encysted larva is eaten by a sheep is development resumed. The larva then escapes and passes into the liver of the sheep, where it matures into adult form.

It will be seen from the above account that a parasite's life-history is considerably complicated to ensure, as far as possible, transmission from one host to another. This can best be effected in two ways:

(i) By producing as many larvae as possible.







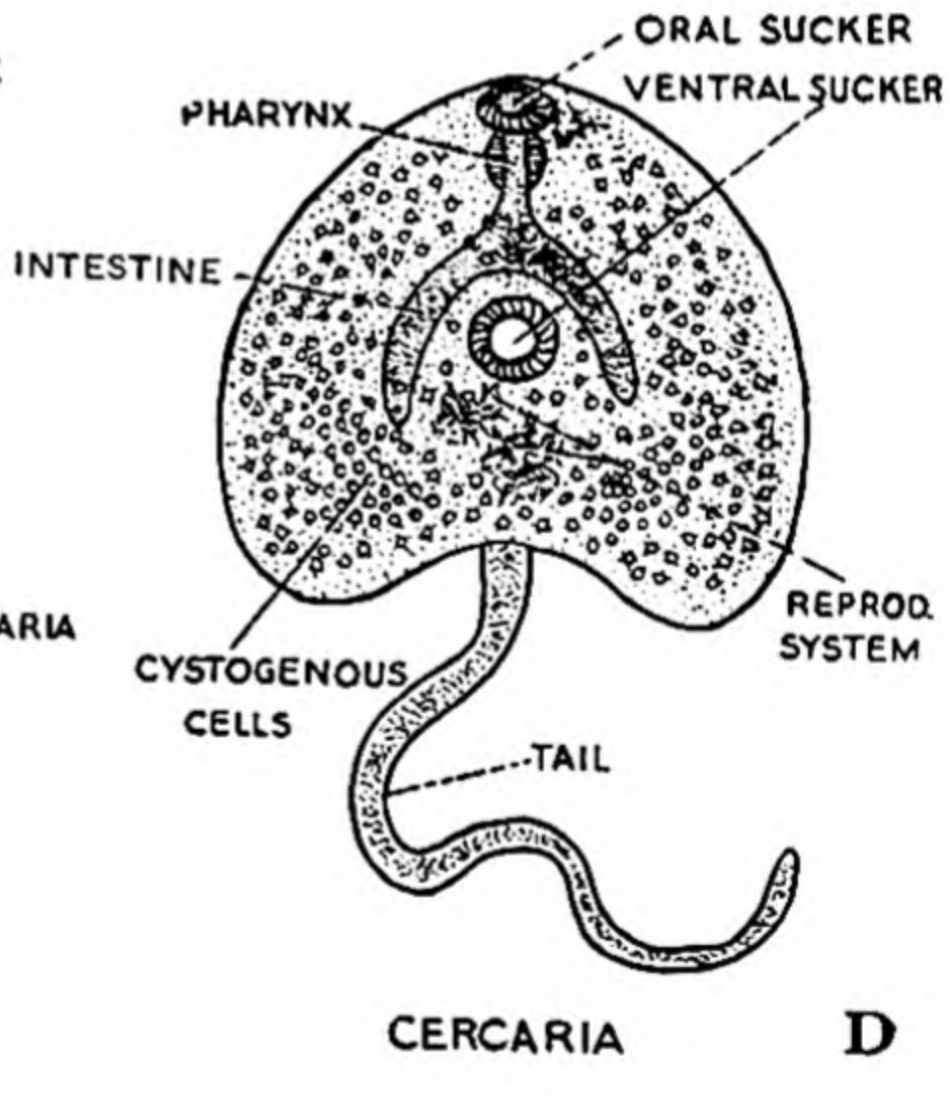


FIG 26 – *Fasciola*. Stages in the life-history.
(From 'Animal Biology', by A. J. Grove and G. E. Newell. University Tutorial Press.)

(ii) By passing some of the intervening period in an intermediate host.

So far as (i) is concerned it will be seen that in *Fasciola* there are three multiplicative phases:

(*a*) The reproductive organs are enormously enlarged so that a very large number of fertilised eggs is produced. Even so it is but very few of them that ever reach the invertebrate host.

(*b*) The germ-cells multiply in the sporocyst and produce rediae.

(*c*) The rediae give rise to several further generations of rediae before they eventually produce cercariae.

With regard to (ii) it is observed that the miracidia develop no further until they have penetrated the body of the invertebrate host. This provides them with a period of shelter, during which rapid reproduction may be effected.

It will be apparent that, in the life-history of *Fasciola*, there is much asexual reproduction, the successive generations of larvae bearing germ-cells which develop by parthenogenesis. The exact nature of this series of multiplicatory phases is open to two possible explanations. It may be a case of **polyembryony**, which involves the origin of many embryos from one fertilised egg. This is an eminently possible explanation, since the propagative cell, cut off from the remainder of the fertilised egg with the formation of first cleavage furrow, is apparently the ultimate source of the whole succession of germ-cells. Alternatively it may represent an instance of **paedogenesis**. This would involve the regarding of the larvae as becoming precociously mature and giving rise to eggs which develop parthenogenetically. The former explanation would appear the more likely, as all the germ-cells appear to arise in continuous succession as products of division of the original propagative cell, being handed on from one larva to another, though their numbers are considerably increased by continued division.

TAENIA

Taenia is a parasite found in the intestine of various mammals. There are several species, according to the host infested, and the one for present consideration is *Taenia solium*, found in the gut of man.

External Characters and Body-wall

As implied by its common name the adult stage of *Taenia solium* takes the form of a flat worm, up to twelve feet in length. Unlike *Fasciola*, but superficially resembling the true worms, or Annelida, it is divided up into a large number of segments, or **proglottides** – as many as a thousand in a fully-grown adult. It must, however, be borne in mind that the interpretation of this so-called segmentation in the Platyhelminthes is vastly different from that in the Annelida. Indeed, it is wise to avoid the usage of this term when speaking of the former phylum. At the extreme

anterior end is the head, or **scolex**. Arranged around this are four large suckers, whilst projecting forwards from it is the **rostellum**, bearing two rings of hooks. The suckers and hooks together effect attachment to the lining of the intestine of the host. Immediately behind the scolex is a narrow neck, connecting this structure with the chain of proglottides, collectively termed the **strobila**. Growth takes place just behind the

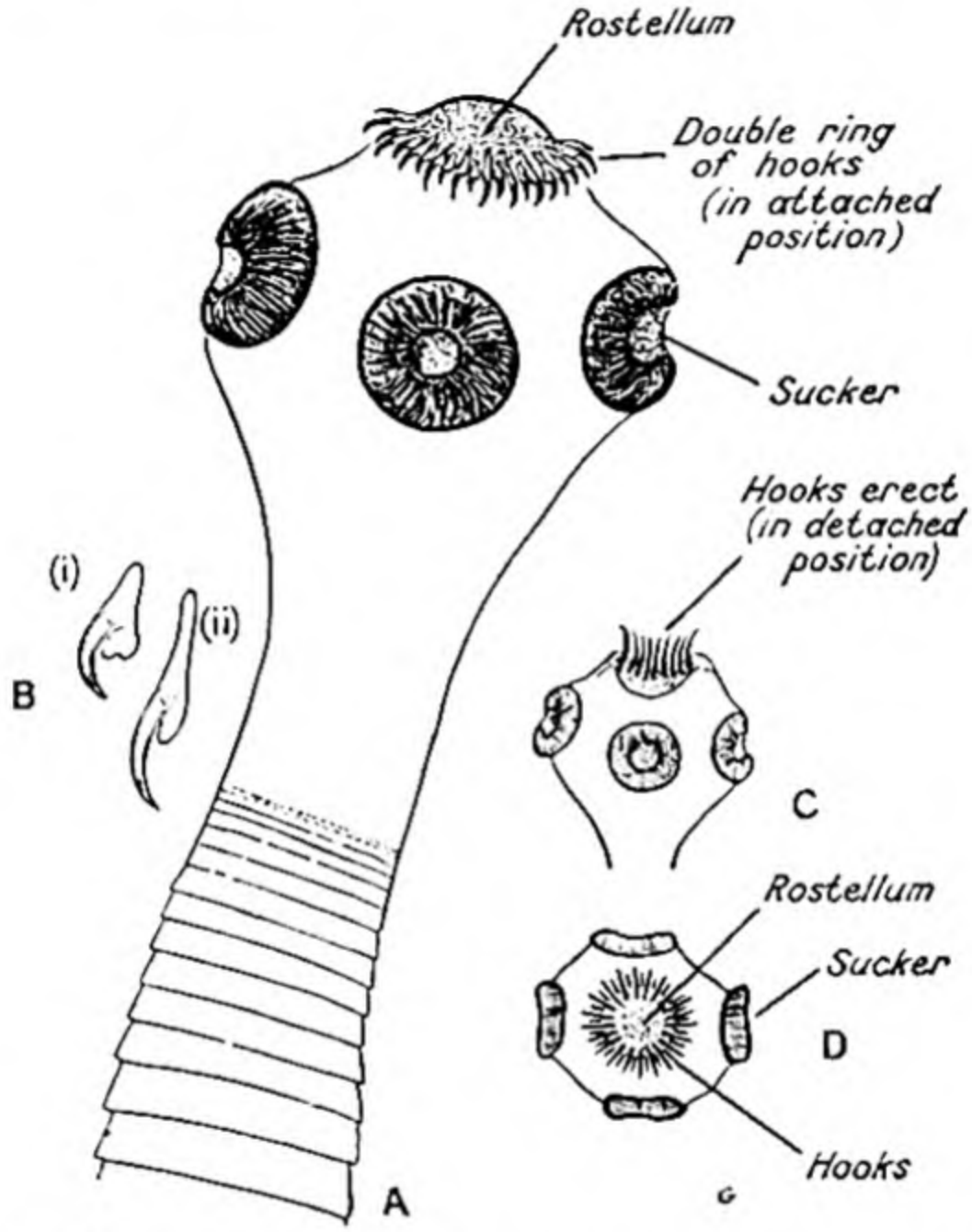


FIG. 27 – *Taenia serrata*. Scolex. *A*, General view of scolex and beginning of chain of proglottides; *B*, Hooks – (i) inner, (ii) outer; *C*, Rostellum withdrawn and hooks erect – in detached position; *D*, Anterior view of scolex, showing arrangement of hooks and suckers.

(*Taenia serrata* is commonly found in the dog, with the cysticercus in the rabbit. It is similar to *T. solium* but is more readily obtained for study.)

scolex, new proglottides being formed. Thus the youngest proglottides lie immediately posterior to the neck, and become progressively older as they are forced towards the hind end. In consequence it is observed that the worm widens posteriorly. The surface is covered with a thick, permeable cuticle, in which occur small channels. The layer immediately within the cuticle is variously interpreted. Some authorities state that

the ectoderm proper disappears at the hexacanth stage (see page 48) and that subsequently a layer of mesenchyme cells is formed at the surface to secrete the cuticle, many of these cells subsiding later into the parenchyma. Alternatively it is claimed that the cuticle is secreted by true ectoderm cells which themselves then sink into the parenchyma. The final appearance is, however, the same. Within the cuticle is a layer of circular muscle, followed by a layer of longitudinal muscle. Deeper in

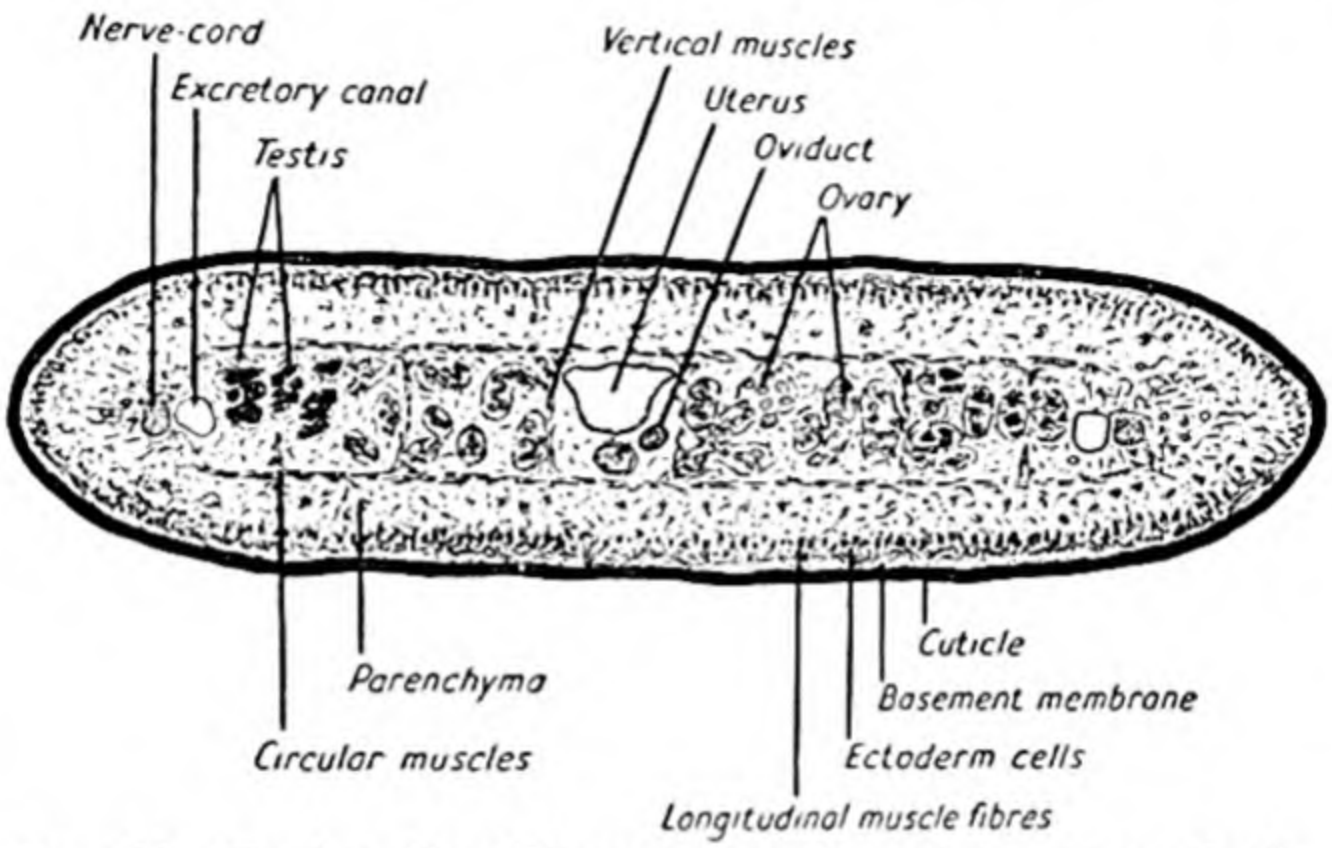


FIG. 28 – *Taenia solium*. Transverse section of a young proglottis.

the parenchyma, approaching from either surface, is a transverse band of muscle, with several vertical bands intersecting them at right angles, as shown in Fig. 28.

Internal Structure

Taenia possesses no gut, and in this respect it may be regarded as degenerate, for an alimentary canal is represented in the majority of the Platyhelminthes. The animal is bathed in the digested food of its host, and this it absorbs over its entire surface. It protects itself from the destructive action of the body-fluids – *e.g.* digestive juices – of its host by means of a calcareous secretion liberated from a number of gland-cells, which occur near the bases of the channels penetrating the cuticle.

Running along either side of the body is a branched tube, the branches ultimately terminating in flame-cells (page 40). These flame-cells collect liquid waste matter from the parenchyma of the animal, from where it is passed into the two collecting ducts, which themselves open to the exterior at the posterior end of the last proglottis. At the posterior end of each proglottis the two longitudinal collecting ducts are united by a transverse canal.

There is a pair of **cerebral ganglia** situated in the scolex and joined

by a dorsal **cerebral commissure.** These ganglia are connected anteriorly with a nerve-ring in the scolex, and there are paired lateral nerve-cords, running through the entire length of the animal and joined in each proglottis by a hoop.

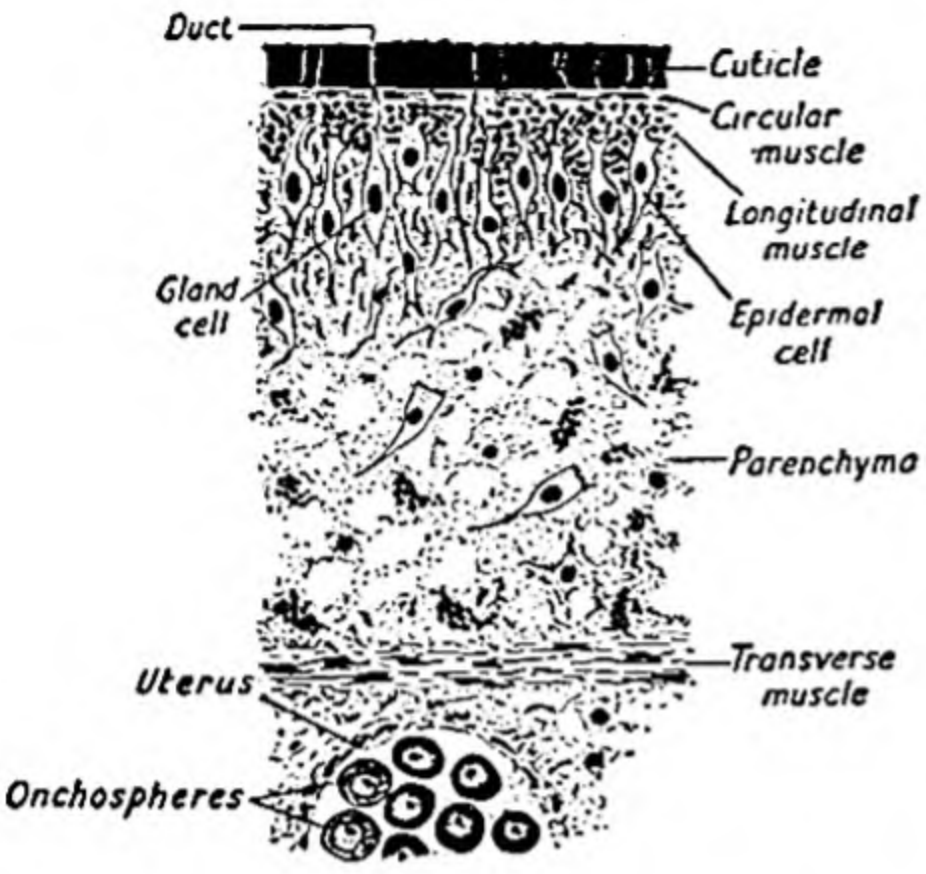


FIG. 29 – *Taenia solium.* Small portion of a proglottis in transverse section, greatly magnified.

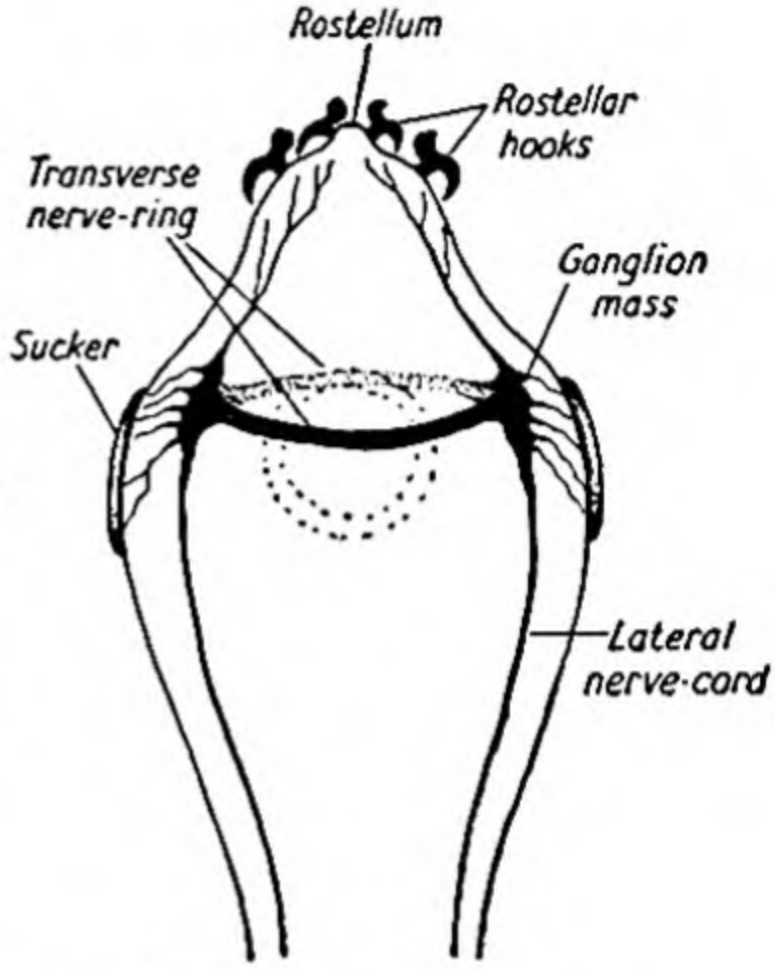


FIG. 30 – *Taenia solium.* Nervous system.

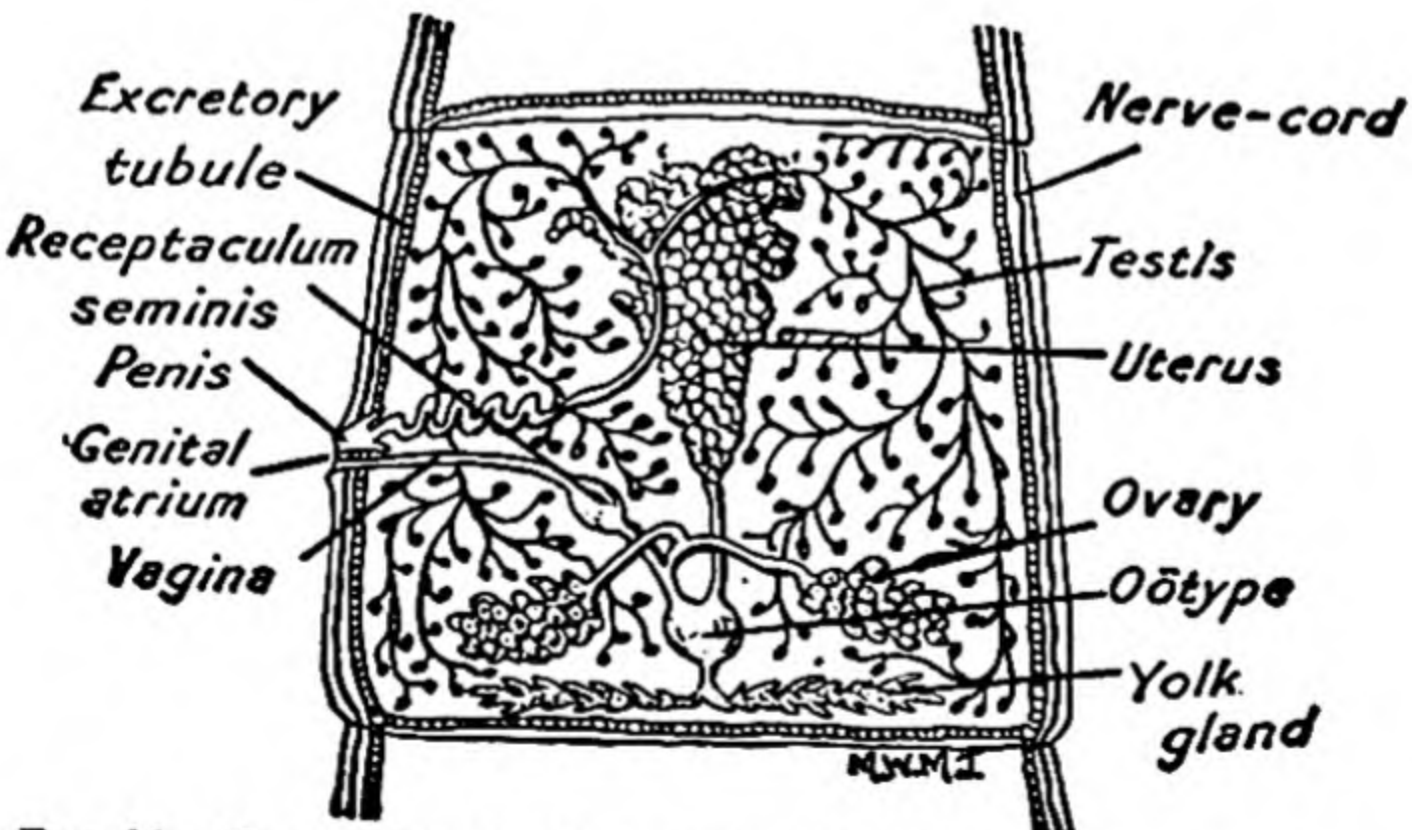


FIG. 31 – *Taenia.* Reproductive organs of a single proglottis. This is idealised to the extent that in the organism male and female organs do not mature together in any one proglottis.

Taenia, like *Fasciola*, is hermaphrodite, though the male and female organs do not mature at equal rates. Accordingly the testes are found

fully developed in the more anterior proglottides, whilst posteriorly the female organs come to occupy almost all the available space. When ripe, the testis is a diffuse organ scattered throughout almost the whole proglottis, the ducts eventually uniting to form a single **sperm-duct**. This terminates in a muscular penis, opening into a genital atrium, which is itself a lateral invagination of the body-wall, opening to the exterior by a hermaphrodite pore. There are two ovaries, each more or less compact and leading by a short oviduct into a spherical chamber, known as an **oötype**. Into this a number of **shell-glands** discharge their secretion. At the posterior end of each proglottis is a diffuse **yolk-gland**, whose secretion is conveyed along a yolk-duct into the oötype. Extending forwards from the oötype is a wide, blind diverticulum, known as the **uterus**, whilst connecting the oötype with the genital atrium is a narrow **vagina**.

Life-history

Spermatozoa from the testes are normally shed into the genital atrium, from which they pass along the vagina into the oötype. When the ripe eggs appear in the oötype they are fertilised by these spermatozoa, so that here self-fertilisation is the rule. Cases are known of fertilisation between different proglottides of the same worm, and actual cross-fertilisation by the shedding of spermatozoa is very difficult to rule out. In the oötype yolk is added to the fertilised eggs, each of which then becomes invested in a horny case, secreted by the shell-glands. The eggs in this condition are passed into the uterus. The more posterior proglottides contain little but uterus, completely distended with eggs, and these proglottides break off from the remainder, a process known as **strobilisation**. They are eventually shed to the exterior with the faeces of the host. Development begins as soon as the eggs are passed into the uterus. The first division results in the separation of a large **vitelline cell** from a smaller **embryonic cell**. The former divides several times, the products acquiring the yolk from the original yolk cell and becoming so placed as to surround the simultaneously dividing embryonic cell, which has by now formed a solid ball of cells, termed the **morula** (Fig. 32, *C*). The single peripheral layer of cells of the morula becomes separated from the main central mass, and this layer secretes a thick, striated, chitinous coat, known as the **embryophore**. The inner mass, meanwhile, develops into an embryo bearing six chitinous hooks, and this is termed the **hexacanth**. The whole structure at this stage, still contained within the egg-case, constitutes the **onchosphere**, and it is with the embryos in this condition that the proglottides are shed. Further development occurs if these encysted bodies are eaten by a pig. The hexacanth is liberated and bores its way into the muscles, frequently those of the tongue, where it becomes a fluid-filled **cysticercus**. The wall of this structure becomes invaginated, and at the base of the invagination a small **proscolex** appears, bearing in its lining the rudimentary hooks and suckers of the future

scolex. This latter becomes evaginated, so that the organs of attachment are brought to the outer surface. If eaten by a man the bladder is digested and the scolex becomes attached to the wall of the alimentary canal.

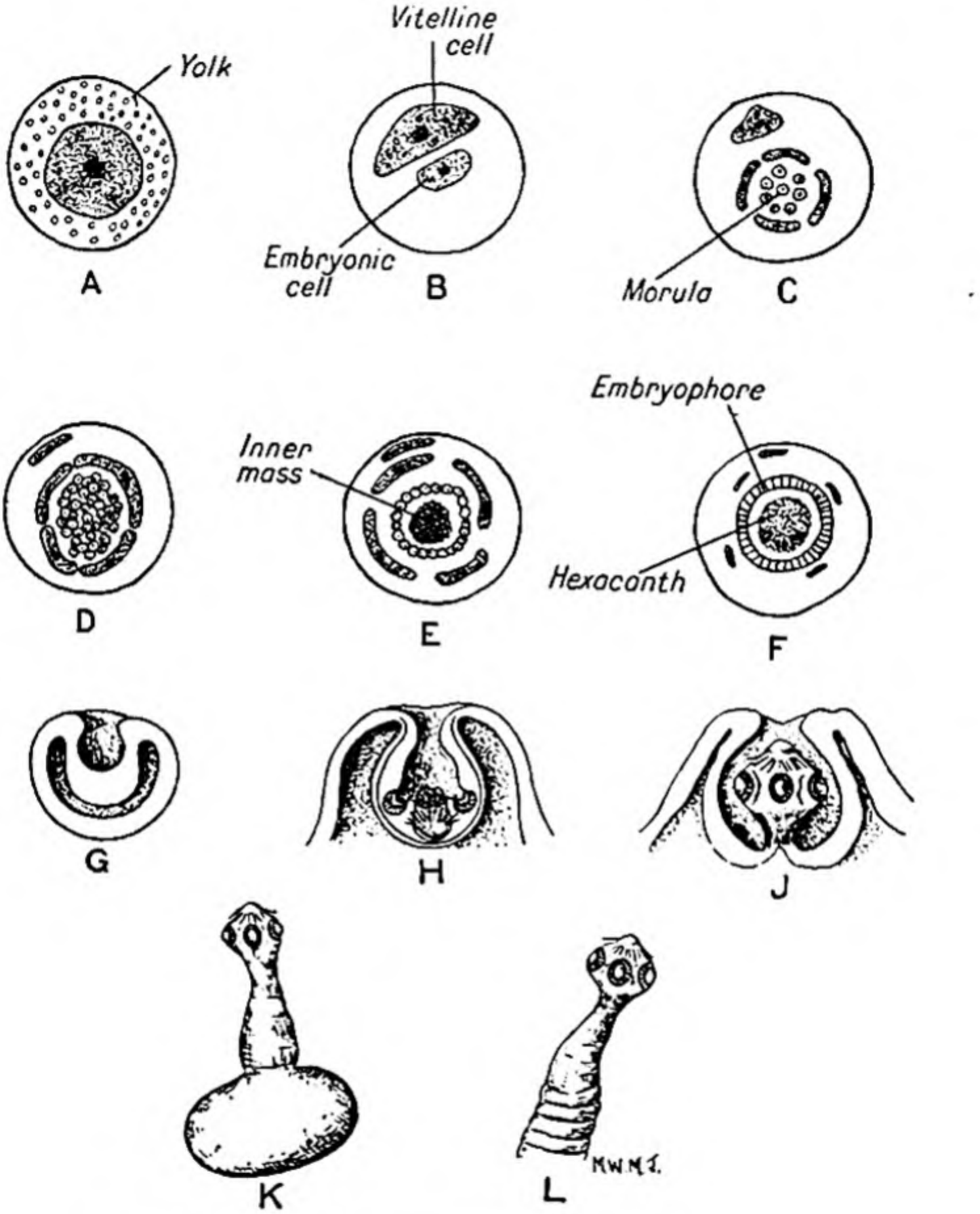


FIG. 32 – *Taenia*. Stages in the life-history.
A., Fertilised egg; *B*., 2-cell stage; *C*., Morula; *D*., Late morula; *E*., Young onchosphere; *F*., Onchosphere; *G*., Early cysticercus; *H*., Later cysticercus; *J*., Scolex everted; *K*., Later; *L*., Early adult. (*A* to *F* after Grove and Newell.)

Proglottides are then formed and a new adult phase is reached. The pig, like the water-snail in the case of *Fasciola*, houses some of the stages between two adult phases in the life-history, and is hence termed

the *intermediate host*. The full life-history may be briefly summarised as follows:

Egg→ onchosphere→ cysticercus→ scolex→ adult.

Parasitic Features

Taking both *Fasciola* and *Taenia* as examples of metazoan parasites, certain fundamental attributes of organisms resorting to this mode of life may be well illustrated. Broadly speaking the distinguishing features of a parasite fall into two categories:

(i) Those in which it is degenerate when compared with free-living members *of the same group*.

(ii) Those in which it is specialised in direct relation to its parasitic habits.

Applying these character-classifications to *Fasciola* and *Taenia* in turn, the former shows relatively little degeneration (when compared with *Planaria*) apart from the absence of surface cilia. *Taenia*, on the other hand, has no mouth or alimentary canal, whilst the ectoderm, in addition to the absence of cilia, has itself greatly degenerated (or disappeared).

Specialisation of actual structure or function in *Fasciola* is not very noticeable, apart from the development of a cuticle. But in *Taenia* there are very significant developments in the form of the scolex, with hooks and suckers for attachment, and the secretion of anti-ferments to protect the body against the digestive juices of the host.

But in most parasites, even in the Protozoa (page 20), the most significant specialisation is in the matter of life-history. Here emphasis must be placed upon numbers to compensate for the hazards involved in the necessity for the infection of new hosts. This characteristic has already been analysed for *Fasciola* (page 42), as has the value of the existence of an intermediate host, biologically associated with the principal host, in effecting the transfer. In *Taenia* the same approach to the problem is found. The most obvious device for the production of vast numbers of fertilised eggs is the continuous proliferation of proglottides, every one of which contains a complete complement of reproductive organs and ultimately reaches the posterior end to be liberated full of embryos. There is, in fact, no further multiplicative phase in the life-history of *Taenia solium*, but a very suitable intermediate host is represented by the pig. It must, however, be realised that with greatly improved standards of sanitation the incidence of the pork tapeworm in man is now greatly reduced.

The presence of a tapeworm produces certain fairly characteristic symptoms in the infected person. Thus the patient is frequently emaciated, whilst anaemia may result from the absorption of vitamin B_{12} by the parasite. Nervous disorders may be caused through the liberation of poisonous substances by the tapeworm. A temporary blockage of the intestine may result from the folding of the tapeworm in so narrow a

cavity. On occasions self-infection may occur – *i.e.* the embryos may be liberated within the gut of the patient instead of being liberated in the faeces. In this case the bladder-worms may come to rest in organs, with the resultant production of serious disabilities. Thus they may settle in the eye and impair vision, or in the brain, where they may be responsible for insanity or epilepsy. Nowadays, *T. sagginata* occurs more commonly than does *T. solium*. Both are basically similar in structure and life-history, but the cysticercoid stage of the former occurs in cattle. Since cattle are normally watered from rivers containing untreated sewage effluent the water which they imbibe is much more likely to be contaminated with tapeworm eggs. Pigs, on the other hand, are more frequently kept enclosed and provided with processed domestic water. Other species of *Taenia* occupy different principal and intermediate hosts. Thus *Taenia serrata* lives in the dog or cat, and has as its corresponding alternative intermediate host the rabbit or mouse. *Taenia metotica* occurs in birds, the earthworm being its intermediate host. *Taenia coenurus* is found in the intestine of certain carnivores, whilst the cysticercoid stage occurs in the brain of sheep, giving them the disease known as 'staggers'. The last two species are interesting on account of the fact that the bladder-worm multiplies by budding, thus enhancing the probability of successful propagation. The same phenomenon is exhibited by *Taenia echinococcus*. The adult stage of this flat worm occurs in the dog, though largely confined to Australia and South America. It is very small, being little more than 5 mms. in length, and consists of a scolex with only two or three proglottides. But the bladder stage, found in the ox, sheep, pig, or occasionally in man, is abnormally large, reaching a diameter of as much as seven inches. Man can become infected by being licked by a dog in which the worms are present, for in this way eggs may get transferred to the mouth unnoticed, possibly contaminating the food. Once within the gut eggs develop to give rise to cysts in various important digestive organs – *e.g.* the liver. The host to some extent protects itself by the formation of a layer of connective tissue about each such bladder, constituting what is known as a **hydatid** cyst. As in some other species the cysticercus multiplies by budding.

PRACTICAL WORK

If available, examine the whole specimens of both *Taenia* and *Fasciola* with a view to discerning the external characters detailed in the text. In the case of *Taenia* concentrate especially on the scolex, examining it under a microscope.

Examine prepared slides of both animals, noticing particularly the structure and disposition of the reproductive organs, as well as the various stages in their life-histories. Draw.

7755

CHAPTER 4

Lumbricus

The earthworm, *Lumbricus terrestris*, belongs to the phylum Annelida, differing from the Platyhelminthes in the possession of a clearly-defined body-cavity, or **coelom**, completely enclosed by mesoderm, a well-developed blood-system, an anus and a characteristic form of nervous system.

Habits and External Characters

The earthworm inhabits the superficial layer of soil rich in decayed vegetable matter, or humus, rarely occurring at depths greater than fifteen inches. There are several species found commonly in England. They live in definite burrows, into which such objects as leaves may be drawn, and the openings may be protected by a number of small stones. In their borings through the soil they increase its porosity, and thus enable water containing dissolved carbon dioxide to reach the solid rock beneath, which consequently becomes partially dissolved, so that they contribute not a little to soil-formation. The loosening effect of these animals on the soil increases its penetrability by the roots of plants, and allows the air necessary for their respiration to circulate more freely. The body of an earthworm is divided into about one hundred and fifty segments. It is cylindrical in shape, slightly blunted at the anterior end and dorso-ventrally compressed posteriorly. The upper, or dorsal, surface is somewhat darker in colour than the lower, or ventral, and the whole body is covered with a slime, secreted by cells of the ectoderm. The mouth is situated at the anterior end, being overhung by a short projection known as the **prostomium**, whilst the anus occurs at the extreme posterior tip. The first segment, since it surrounds the mouth, is known as the **peristomium**. On every segment except the first and last are four pairs of short, stiff bristles, or **chaetae**. They are arranged as one lateral and one ventral pair on each side of the body, and may be distinguished by passing the thumb and finger in a postero-anterior direction along the body, since they are directed slightly backwards. Besides the structures already described there are several important apertures opening on to the surface. On every segment except the first three and the last is a pair of **nephridiopores**, lying just in front of the ventral chaetae; they are the openings of the excretory organs, or nephridia. In the mid-dorsal line of the grooves behind every segment after and including the eighth is a minute **dorsal pore**, leading from the body-cavity, or coelom. The fluid

(coelomic fluid) which escapes from them assists in keeping the surface of the body moist, besides which the minute amoeboid cells contained in this fluid largely protect the skin of the worm from invasion by Bacteria. In each of the depressions, between segments 9 and 10 and 10 and 11 there opens a pair of pocket-like structures, known as the **spermathecae**, whilst the **vasa deferentia**, conveying the sperms to the exterior, open as

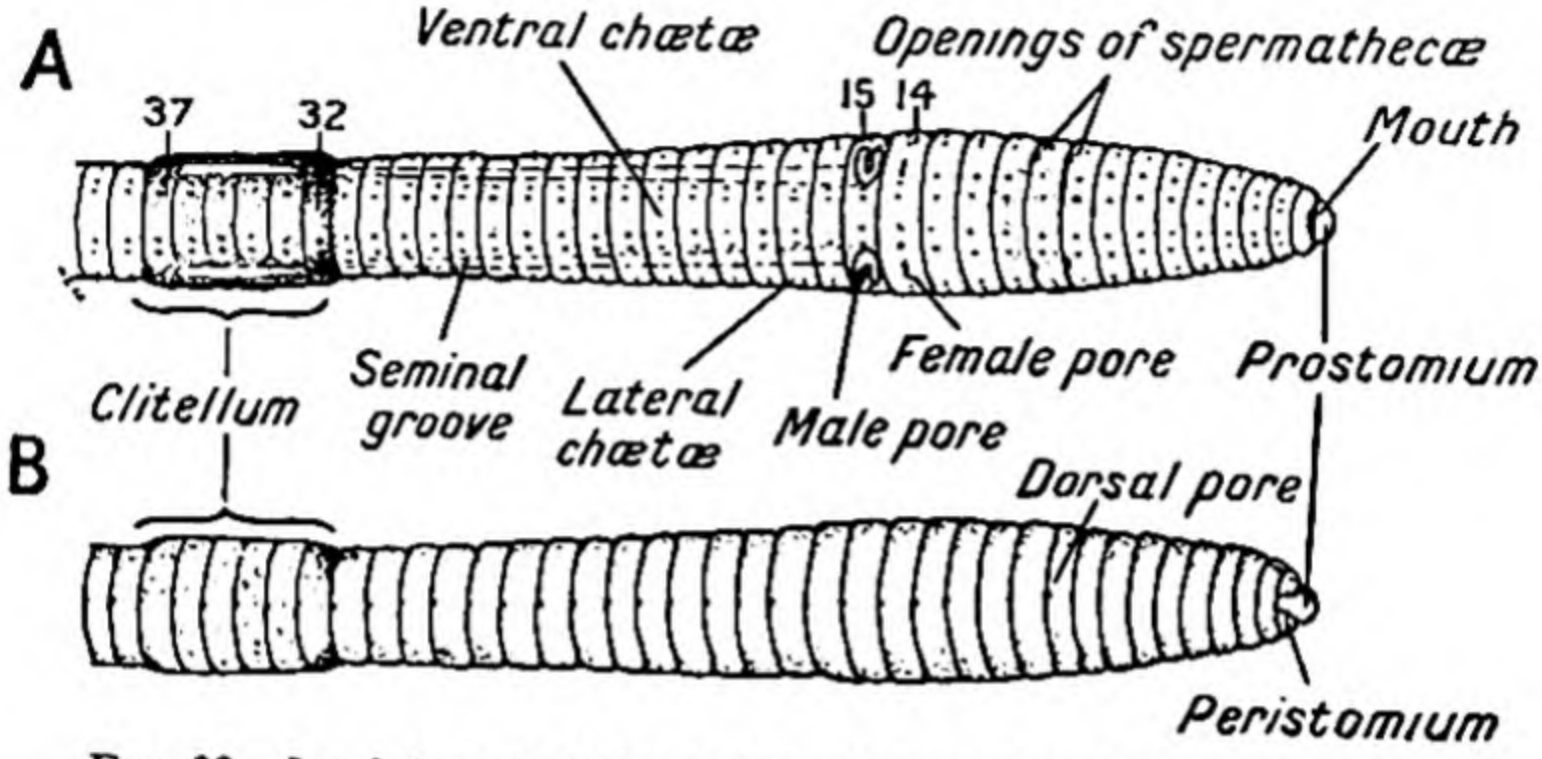


FIG. 33 – *Lumbricus*. Anterior end in *A*, Ventral, and *B*, Dorsal, view.

a pair of slits with swollen lips on the ventral surface of segment 15. The pair of openings of the oviducts appear at the same level of the body in segment 14. Covering segments 32–37 is a glandular band of skin, known as the **clitellum**, the significance of which will be considered later. Except during pairing there are visible two pigmented **seminal grooves**, extending backwards from the male pores on segment 15 to the clitellum.

Body-wall

The whole surface of the body is covered with a thin cuticle, a product of the **epidermis** which lies immediately beneath it. It is perforated at intervals by channels which allow the secretion of the glandular cells of the epidermis to escape. The epidermis itself consists of columnar cells, some of which are concerned in the production of a mucous secretion, whilst others are sensitive to certain stimuli. Immediately within the epidermis is a nerve-plexus, followed by a layer of circular muscle circumventing the whole body, and within this again is a layer of longitudinal muscle. The fibres are arranged in blocks, down the centre of each of which passes a blood-vessel. The whole layer is bordered on the inside by the **coelomic epithelium**, composed of pavement cells and forming a lining to the outer wall of the body-cavity. Each chaeta is set into the body-wall as shown in Fig. 34. It is composed of a chitin-like substance and secreted by a single formative cell at its base. It lies within the epidermal **chaetigerous sac**, and its movements are controlled by retractor and protractor muscles.

The body of the earthworm may be regarded as consisting of two hollow, concentric cylinders, for within the cylinder already described, and separated from it by a space, known as the **coelom** and containing coelomic fluid, is the gut or alimentary canal. This is itself enclosed by a

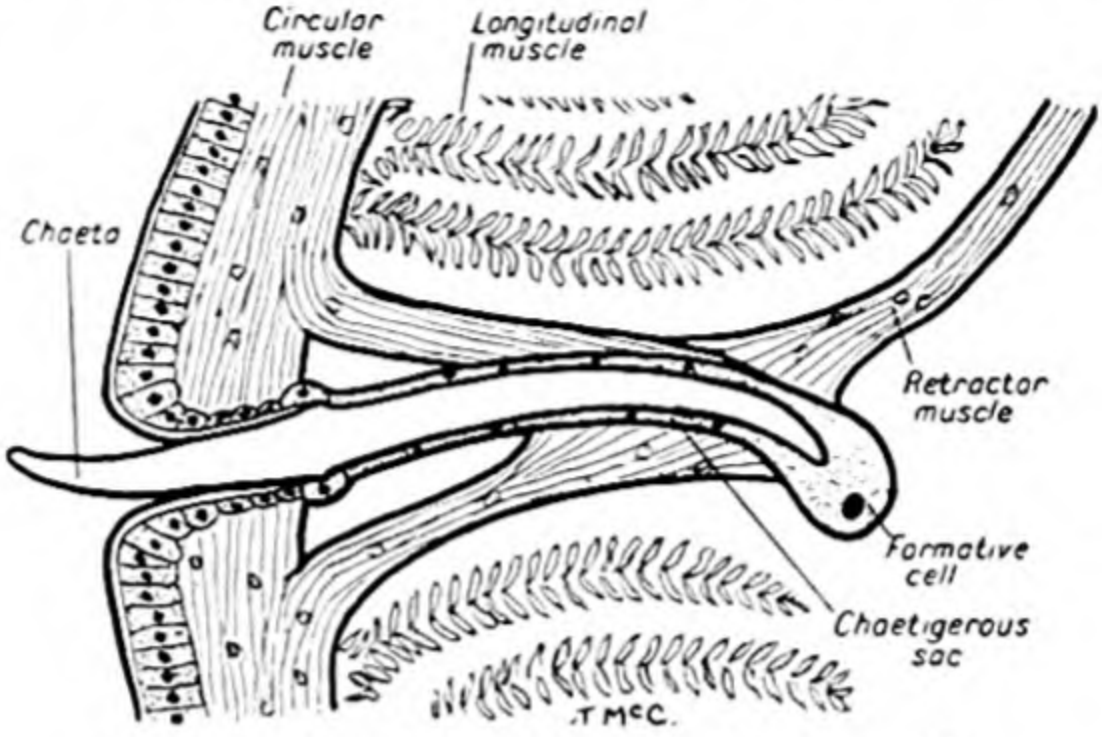


FIG. 34 – *Lumbricus*. Section of body-wall to show insertion of a chaeta.

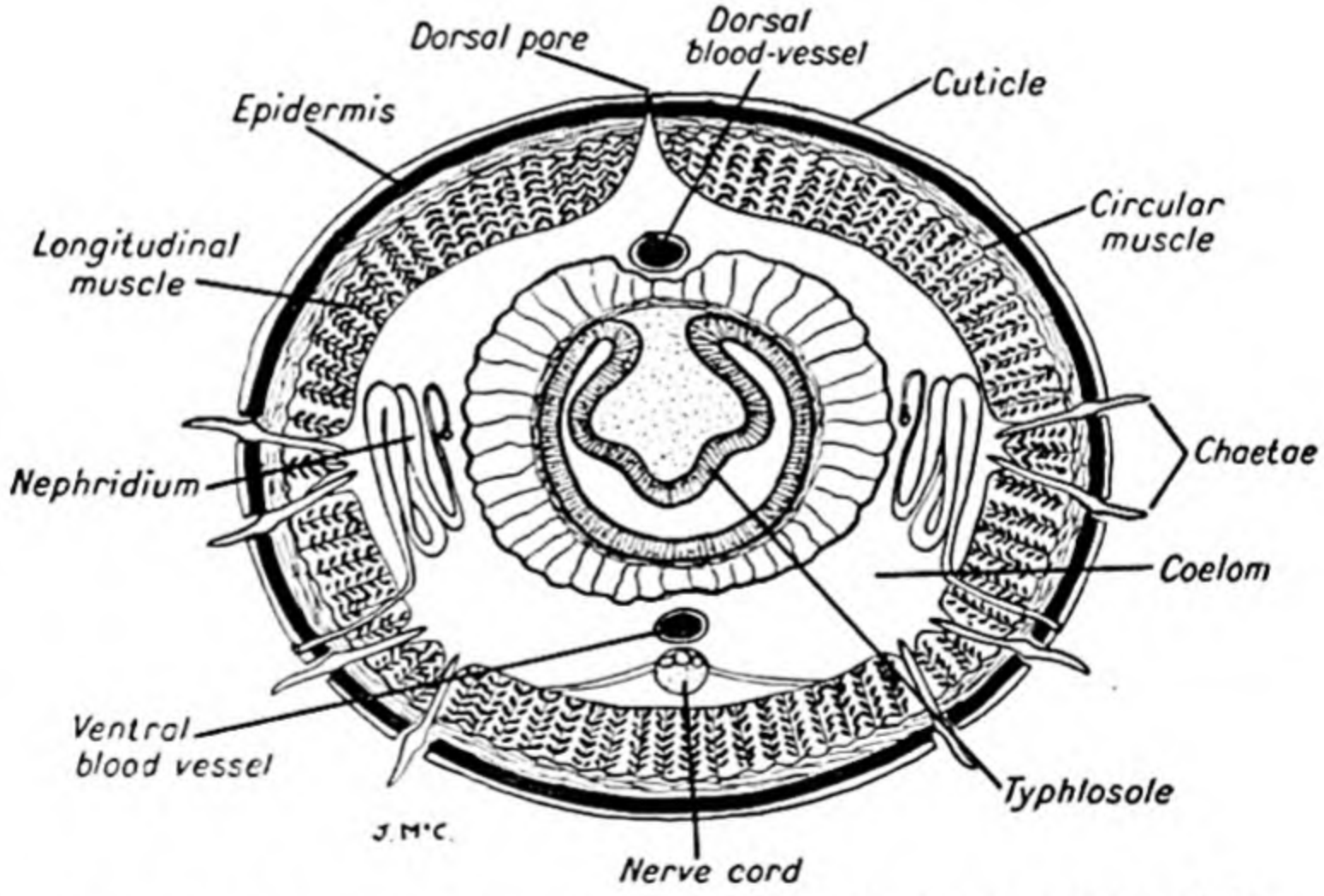


FIG. 35 – *Lumbricus*. Transverse section of the body in the region of the intestine (somewhat diagrammatic).

layer of coelomic epithelium, which, in the region of the intestine, is in the form of large, yellow, cells, termed the **chloragogenous tissue**. Within this is a thin layer of longitudinal muscle, followed by a layer of circular muscle. The lumen of the gut is bordered by endoderm. It is further

observed in the region of the intestine that the dorsal side of the gut, with its surrounding coats of muscle, is invaginated, the invagination being known as the **typhlosole** and filled with chloragogenous cells. In

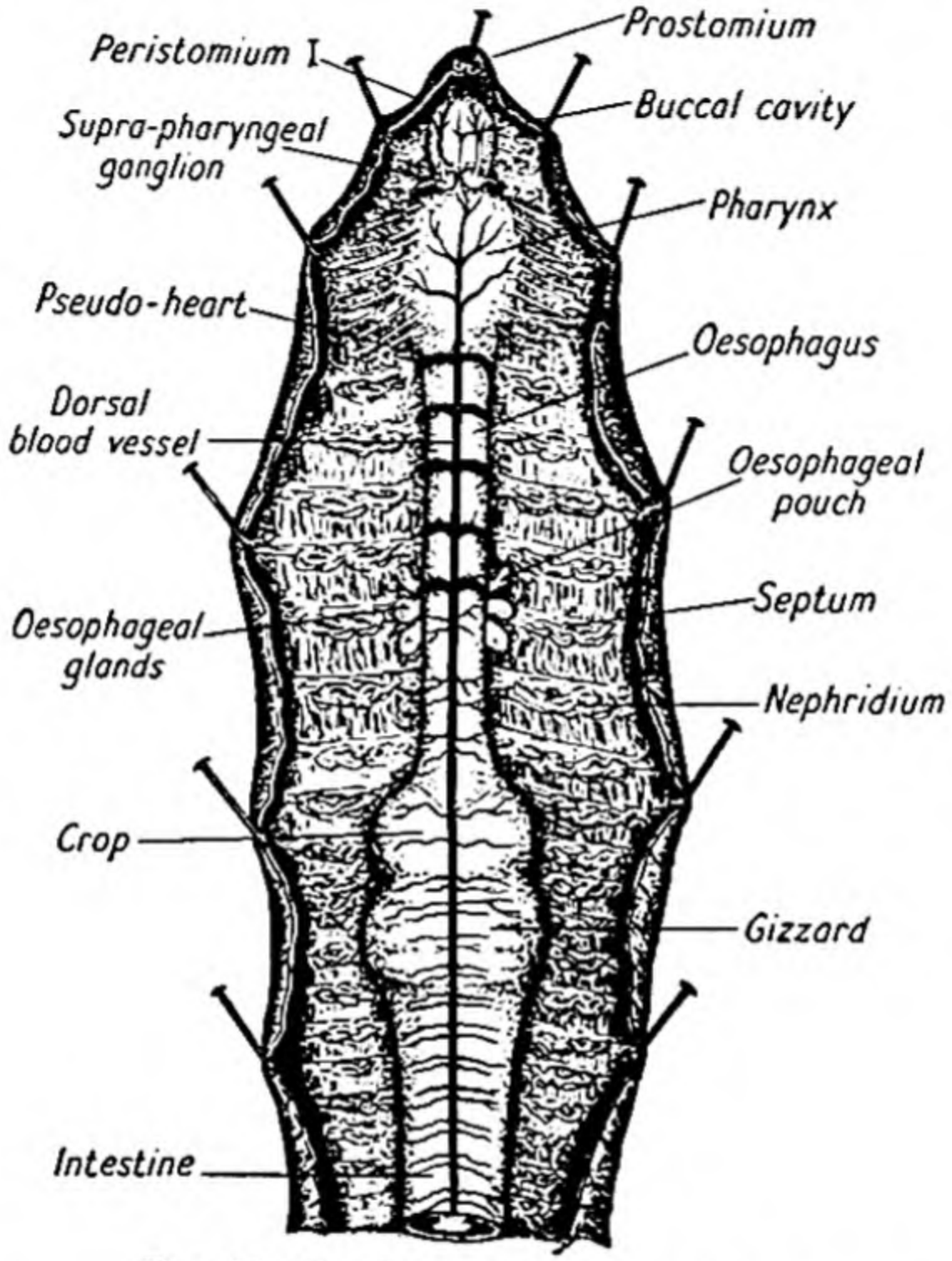


FIG. 36 – *Lumbricus*. Alimentary system.

these cells runs the dorsal blood-vessel. The body-cavity, or coelom, is interrupted by a number of **septa**, these corresponding in position to the grooves dividing the body into segments externally. Each septum consists of a double layer of coelomic epithelium, with a thin sheet of muscle between the layers. These septa form a support for the alimentary canal, and are perforated also by the blood-vessels, nerve-cord and nephridia.

Alimentary System

The alimentary canal is a straight tube, extending from the mouth to the anus and showing a certain amount of regional differentiation. The mouth opens into a thin-walled **buccal cavity**, occupying the first three segments. This leads into a muscular **pharynx**, situated in the fourth to the sixth segments. The dorsal wall of this region produces a digestive

juice which digests proteins. The pharynx leads into the **oesophagus**, a thin-walled, narrow, partially-ciliated tube extending from the seventh to the fourteenth segments. In the eleventh and twelfth segments are two pairs of lateral **oesophageal glands.** These produce calcium carbonate, which is passed into a pair of pouches opening into the gut in the tenth segment. In segments 15 and 16 is an expanded **crop**, where food may be temporarily stored. From here it is passed into a thick-walled, muscular **gizzard**, with a horny lining, where mastication occurs. The remainder of the gut consists of a thin-walled **intestine**, invaginated to form a typhlosole as already indicated. The chloragogenous cells in this region become loaded with waste matter and eventually fragment into the coelom, from which their products are eliminated. The lining of the intestine produces further digestive juices.

Food is drawn into the early part of the alimentary canal by the suctorial action of the muscular pharynx. This same region is also responsible for propulsion of food through the oesophagus which, from time to time, exhibits lateral folds. Calcium carbonate is wafted backwards in the form of microcrystalline particles by the oesophageal cilia to the crop, causing flocculation of the soil. The gizzard, as well as effecting some mastication, acts as an accessory pump to maintain the food in motion through the intestine, in which capacity it is doubtless assisted by movements of the body-wall, causing variations in the pressure of coelomic fluid on the intestinal wall. The passage is further eased by the lubricating action of mucus secreted by the endothelium (page 329) of the typhlosole. Only the humus of the soil is of nutritive value, the undigested remains being shed through the anus as *worm casts*. It is estimated that, as a result of this activity, earthworms bring to the surface some twenty-five tons of finely-divided soil per acre of arable land per annum.

Vascular System

This system is well developed in *Lumbricus* and is composed of a series of vessels united at capillaries. Thus the system is described as *closed.* The three principal vessels run longitudinally, virtually throughout the entire length of the animal, and according to their position they are termed the dorsal, the ventral and the sub-neural vessels. The **dorsal** vessel is primarily one into which blood is collected, the blood flowing forwards in it. From its anterior end blood is distributed to the wall of the pharynx and buccal cavity, whilst in the intestinal region it supplies the typhlosole. In each of segments 7 to 11 is a pair of **pseudo-hearts**, circumventing the oesophagus to connect the dorsal with the **ventral** vessel. This is the principal distributory channel, along which blood flows backwards. From it there arises, in every segment, a pair of **ventro-parietal** vessels to supply the body-wall, nephridia and reproductive

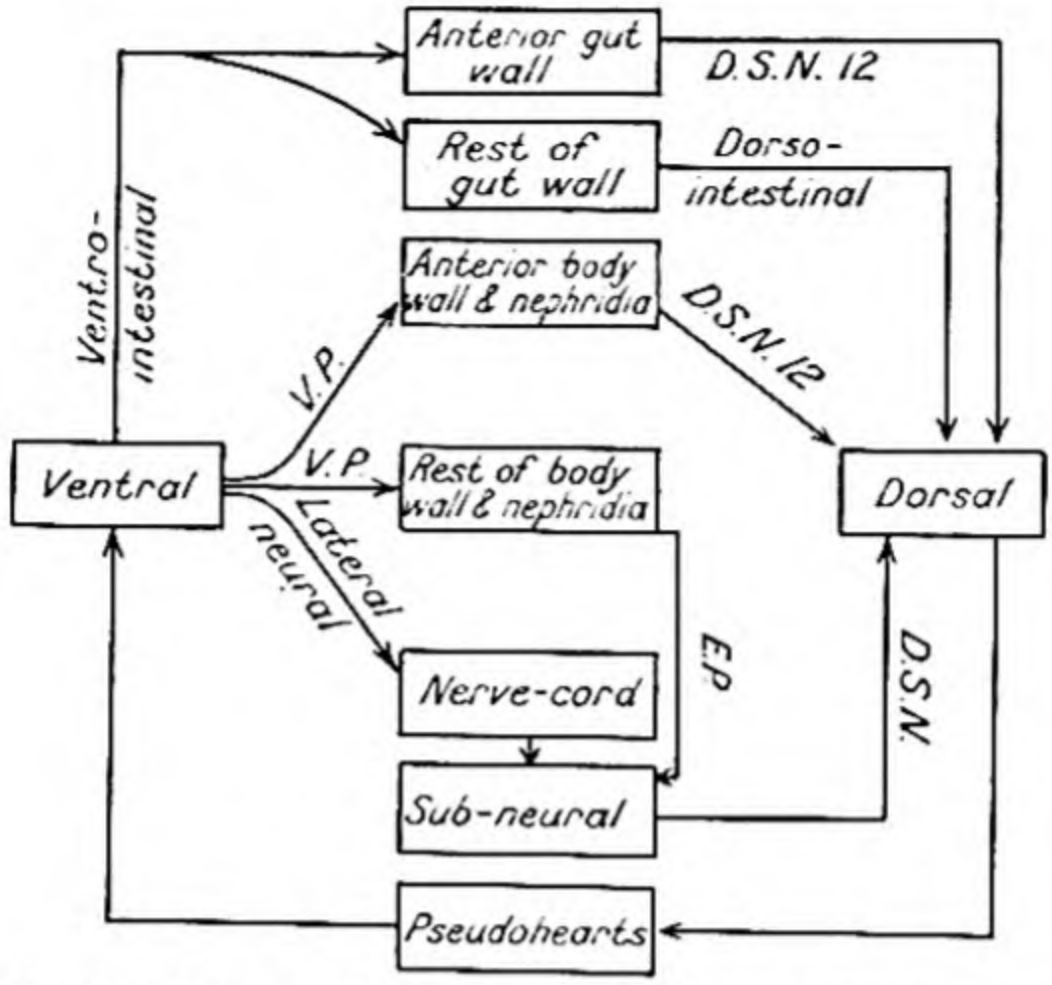


FIG. 37 – *Lumbricus*. Plan of blood-circulation. *D.S.N.*, Dorso-sub-neurals; *E.P.*, Efferent parietals; *V.P.*, ventro-parietals.

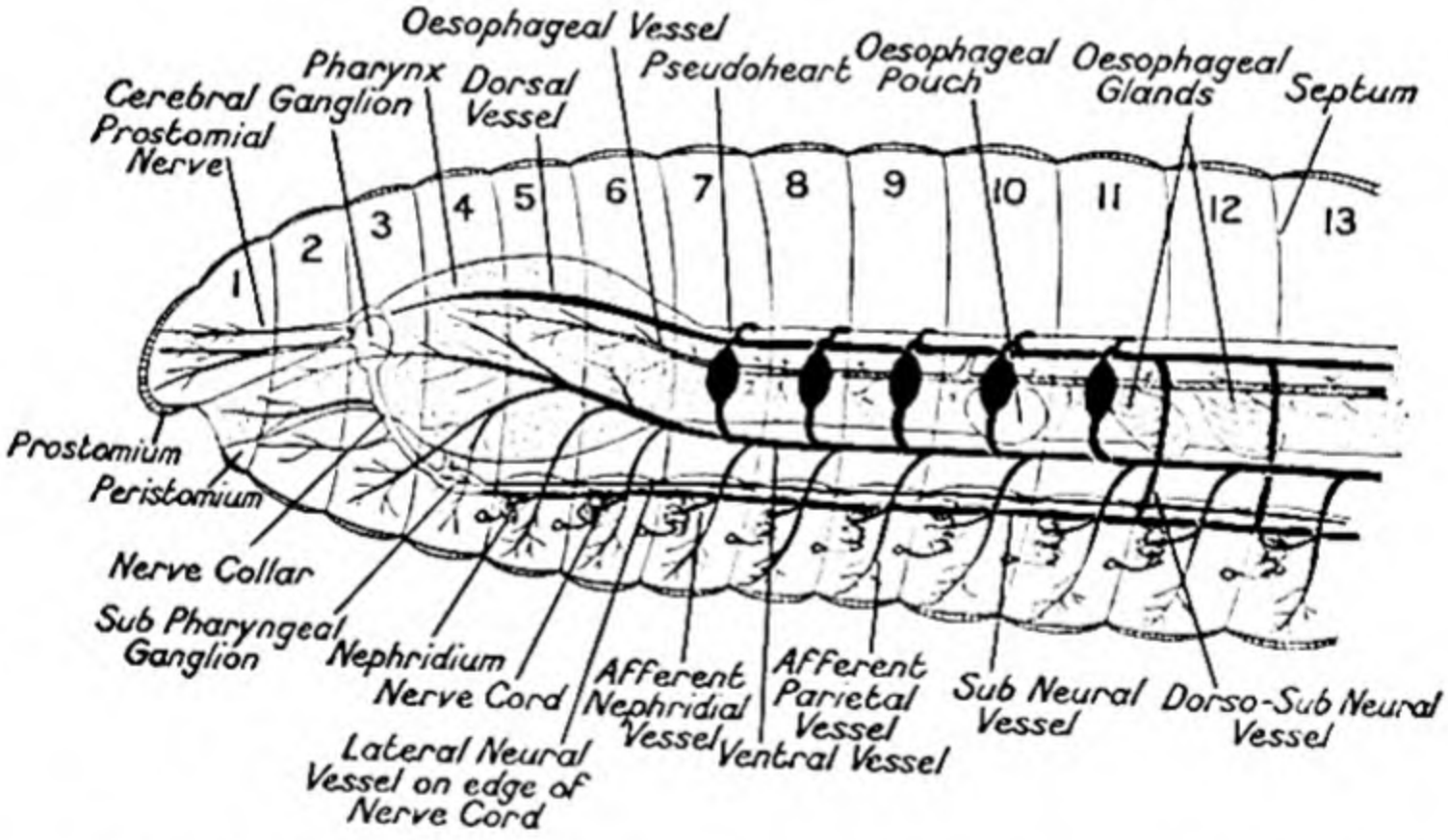


FIG. 38 – *Lumbricus*. Lateral view of anterior end, showing principal blood-vessels. (From 'Invertebrate Types', by T. A. G. Wells.)

organs, whilst inter-segmental pairs of **ventro-intestinal** vessels vascularise the gut-wall. From these organs, from segment 12 backwards, **efferent parietals** drain blood into the **sub-neural** vessel, which is itself connected with the dorsal vessel by paired, segmental **dorso-sub-neurals.** From the same organs anterior to segment 12 and from the entire oesophagus blood is collected into a vessel on either side of the oesophagus, these in turn discharging partly into the dorso-sub-neural of

segment 12 and partly into the dorsal vessel in that segment. **Dorso-intestinal** vessels carry blood from the gut-wall to the dorsal vessel in the intestinal region, whilst the part of the gut anterior to this also has its blood conveyed to the dorso-sub-neural vessel of segment 12. The nerve-cord is rather specially catered for. Running along either side of the nerve-cord is a **lateral neural** vessel, which receives blood from the ventral vessel for supply to the nerve-cord, from which blood is drained directly into the sub-neural vessel. The main features of this rather complex system are represented schematically in Fig. 37 and diagrammatically in Fig. 38.

Circulation is maintained by rhythmic, pulsating movements of the dorsal vessel and the pseudo-hearts, whilst valves, present in the hearts and the inlets of the principal tributaries into the dorsal vessel, prevent back-flow. Thus the vessels cannot fairly be discriminated into arteries and veins. The blood itself contains haemoglobin in solution and also numerous leucocytes.

Respiration

Respiration is effected by gaseous exchange through the surface. It is especially important in this respect that the body be kept moist, for this readily faciliatates an exchange. Oxygen is absorbed through the surface of the body into the capillaries of the skin, where the haemoglobin is oxygenated to form oxy-haemoglobin. This compound dissociates on reaching tissues deficient in oxygen, and the waste carbon dioxide is carried away in solution in the plasma to be expelled through the surface of the animal.

Locomotion

In order to move forwards the earthworm first anchors its hind end

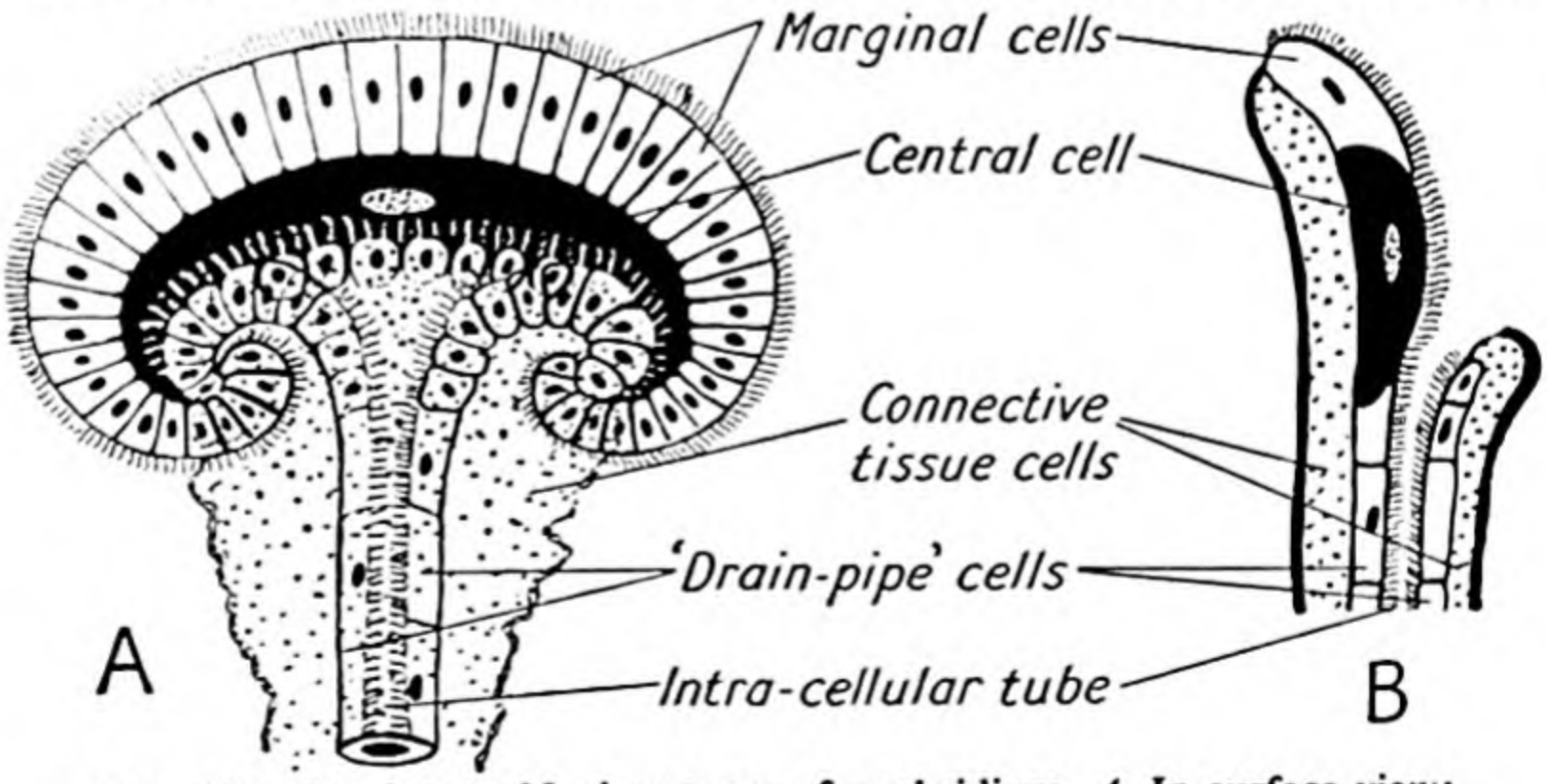


FIG. 39 – *Lumbricus*. Nephrostome of nephridium. *A*, In surface view; *B*, In longitudinal section.

by means of the chaetae in that region. It then contracts the circular muscles of the body-wall. This results in an increase in length, since the cross-sectional area must become reduced, yet the volume remains unchanged. The animal then attaches its front end by means of chaetae and releases the hind end. The circular muscles are now relaxed and the longitudinal muscles contracted. In consequence the hind end is drawn forwards. By alternately attaching and releasing points nearer together than the extreme front and hind ends any median portion of the animal may thus be extended, and waves of muscular contraction may be observed normally to pass along the body from front to hind end.

Excretory System

It has already been pointed out that the cavity separating the body-wall from the gut is filled with a fluid. Into this fluid all the liquid waste matter is collected as, for instance, by the disintegration of the chlorago-

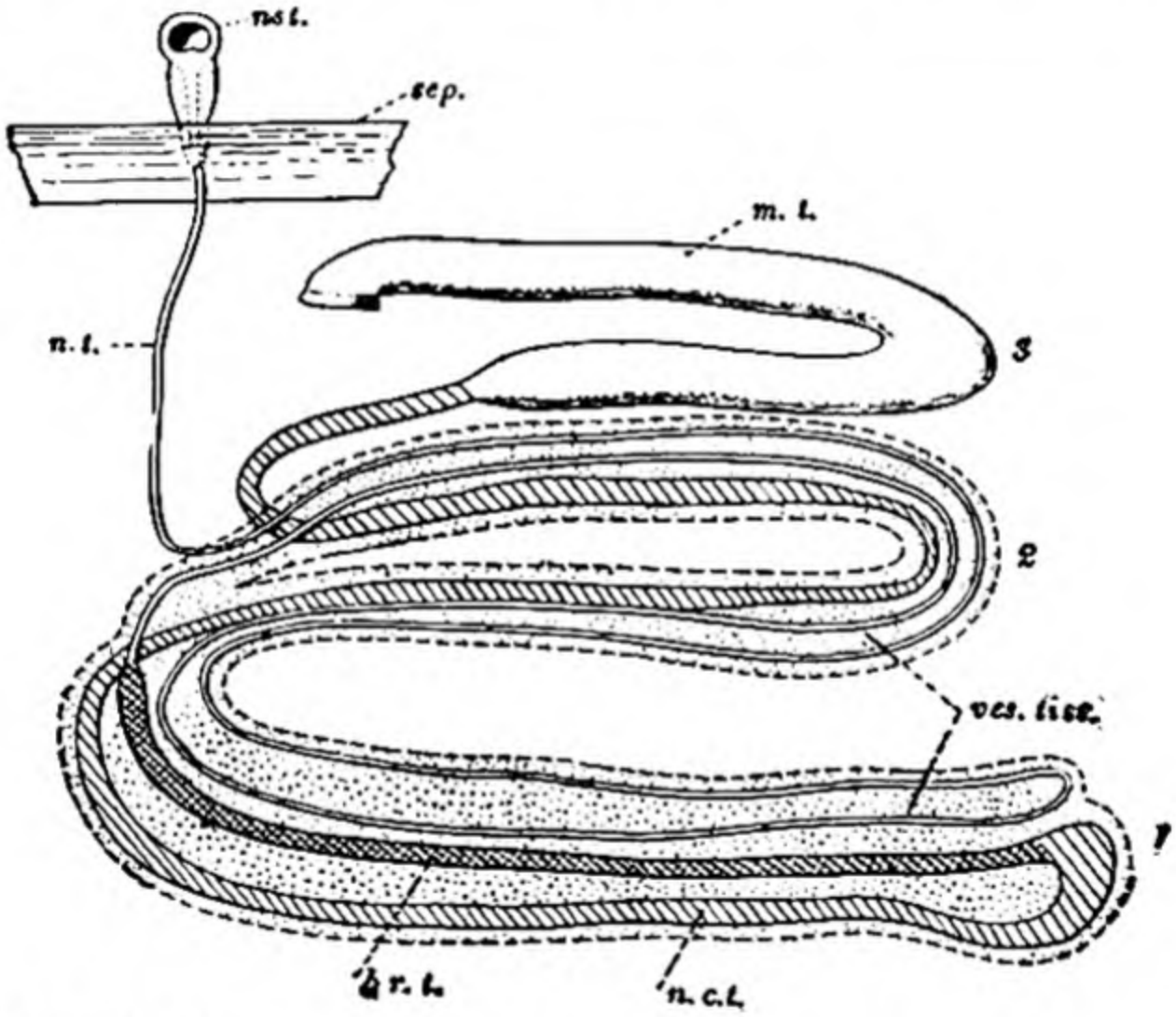


FIG. 40 – Diagram of nephridium of Earthworm. (From 'Manual of Zoology', by L. A. Borradaile. O.U.P.)
br.t., brown, ciliated tube; *m.t.*, muscular tube; *n.c.t.*, glandular, non-ciliated tube; *n.t.*, narrow tube, ciliated in parts; *nst.*, nephrostome; *sep.*, septum; *ves.tiss.*, connective tissue; 1, 2, 3, the three hanks of the tube.

genous cells into the coelom. Some small part of this fluid is exuded through the dorsal pores, but the organs mostly concerned with its purification are the **nephridia**, of which there is a pair in all segments except the first three and the last. A nephridium is a much-coiled tube, com-

mencing as a ciliated funnel, or **nephrostome**, just in front of each septum, which it almost immediately penetrates, so that the bulk of the organ lies in the next posterior segment, from which it opens to the outside by a **nephridiopore**. The nephrostome takes the form of a flattened funnel, the larger upper lip of which is composed of a single *central* cell, fringed by a series of ciliated *marginal* cells (Fig. 39 *A*). The lower lip is composed of small, non-ciliated cells. The tube itself shows a certain degree of regional specialisation. Just behind the nephrostome is a ciliated tube which penetrates the septum. Once in this segment the nephridium continues its course still as a narrow, partially-ciliated tube, and this gives place to a wider, ciliated, brown tube. This leads into a wider, non-ciliated tube, and finally the liquid waste matter is conveyed to the nephridiopore by a much wider, muscular tube. The whole structure is bound together by connective tissue into three distinct banks, whilst, except in the muscular region, the tube consists of hollow cells joined endwise. The liquids are kept in motion by the beating of the cilia, but the cells constituting a nephridium are actively excretory, and not merely passive channels, being richly supplied with blood-capillaries from which they extract waste products. The principal nitrogenous excretory product is guanin, which is also extracted directly from the blood by the 'brown tube' component of the nephridia. In addition, some uric acid is excreted, mainly from the cells of the coelomic epithelium covering the gut. Amoebocytes also assist in this important function. Floating freely in the blood, they are eventually discharged into the lumen of the gut, from which they and their contained waste matter are eliminated through the anus. In arid conditions the nephridiopores can be closed by sphincter muscles, leading to the conservation of water.

Nervous System

The nervous system of the earthworm is well developed. It is built on a plan characteristic of almost all invertebrates above the Platyhelminthes. It consists of two **supra-pharyngeal ganglia**, connected by two **peri-pharyngeal commissures** with a ventral nerve-cord, which runs throughout the length of the animal. Prostomial nerves arise from the supra-pharyngeal ganglia and peristomial nerves from the commissures. The first segmental ganglion of the nerve-cord is found in segment 4 and from it segments 2, 3 and 4 are innervated. Subsequently the nerve-cord, in every succeeding segment, bears three pairs of nerves, two arising from the ganglion and one anterior to it. Every nerve divides into a short ventral branch and an elongated dorsal branch, the paired dorsal branches forming almost complete rings and communicating with the nerve-nets, of which there are two – one below the epidermis and one between the muscle-layers. A further nerve-net is to be found in the gut-wall and this is connected by six pairs of nerves with the peri-pharyngeal commissures.

The supra-pharyngeal ganglia serve mainly for the relay of impulses arising from the receptors (see below) at the anterior end of the body. Accordingly they consist largely of nerve-cells whose processes connect the fibres of the receptors with the ventral nerve-cord. The dorsal part of the nerve-cord consists principally of nerve-fibres, above the general mass of which are three **giant fibres**. These run the entire length of the animal and each consists of a collection of nerve-fibres, with synaptic connexions in every segment, where communication is established with the musculature of that segment, as well as with the giant fibres in the segment next behind. Thus collectively the giant fibres are responsible for the wholesale response of the animal to drastic stimulation. Ventrally the nerve-cord is composed mainly of nerve-cells, from which run fibres to the musculature. Particularly large cells – **giant cells** – in every segment are connected with the giant fibres. Thus there is, in the nerve-cord, an approximate discrimination into sensory and motor areas. The fibres in the dorsal region are contiguous with the sub-epidermal nerve-net and are therefore presumably sensory, whilst ventrally the cells bear fibres which run to the musculature and hence may be described as motor (page 462).

Sense Organs

Though not very highly developed, two varieties of external sense organ may be recognised in *Lumbricus*. Those of the simpler type consist of single epidermal cells, whose outer surface is produced into processes extending beyond the cuticle, whilst the base of such a cell is continued inwards to reach the nerve plexus beneath the epidermis. Most of these organs are tactile, though possibly some of them may be chemo-receptors. The earthworm is very sensitive to ground vibrations.

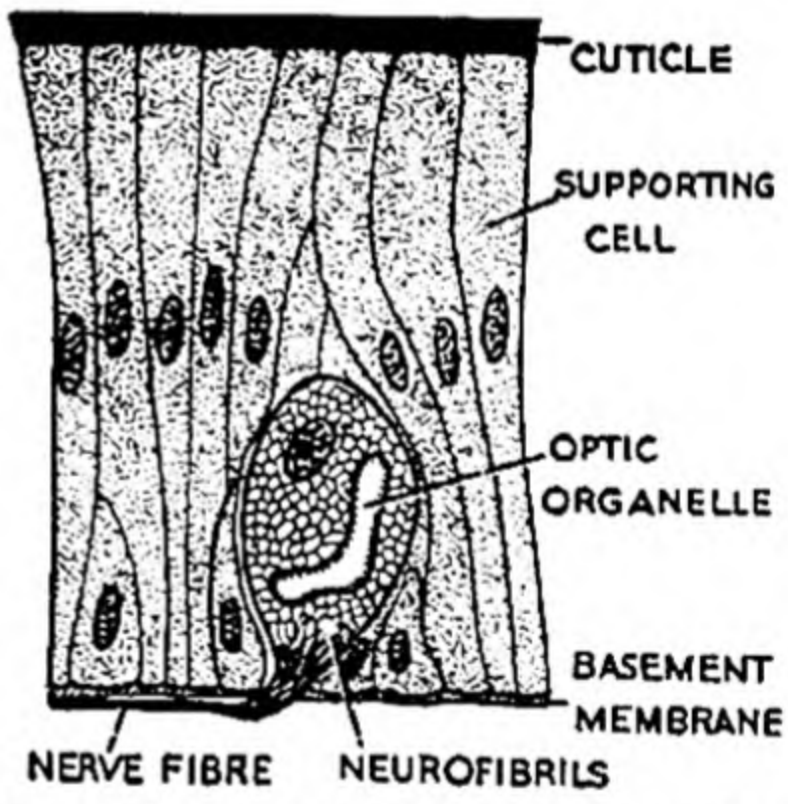


FIG. 41 – *Lumbricus*. Vertical section of the epidermis with a photo-receptor. (From 'Animal Biology', by A. J. Grove and G. E. Newell. University Tutorial Press.)

The photo-receptor organs are rather more complex. They are situated deep in the epidermis of the prostomium, and each consists of a large, transparent cell, containing a colourless rod, termed the **optic organelle**. This presumably functions to focus light on to the sensitive fibres at the base, and these ultimately convey the impulses to the ganglia.

It is to be assumed that proprioceptors (page 465) exist for the control of muscular activity and other changes *inside* the body.

Reproductive System

Lumbricus is hermaphrodite – *i.e.* each individual bears both male and female reproductive organs. The ovaries are a pair of pear-shaped bodies, situated on the anterior septum of the thirteenth segment. Each is formed by a thickening of the coelomic epithelium in that region. From the ovary developing eggs are shed into the coelom at the oöcyte stage (page 319), maturing subsequently. From this cavity their only means of escape is via one of the pair of **oviducal funnels**. These are situated

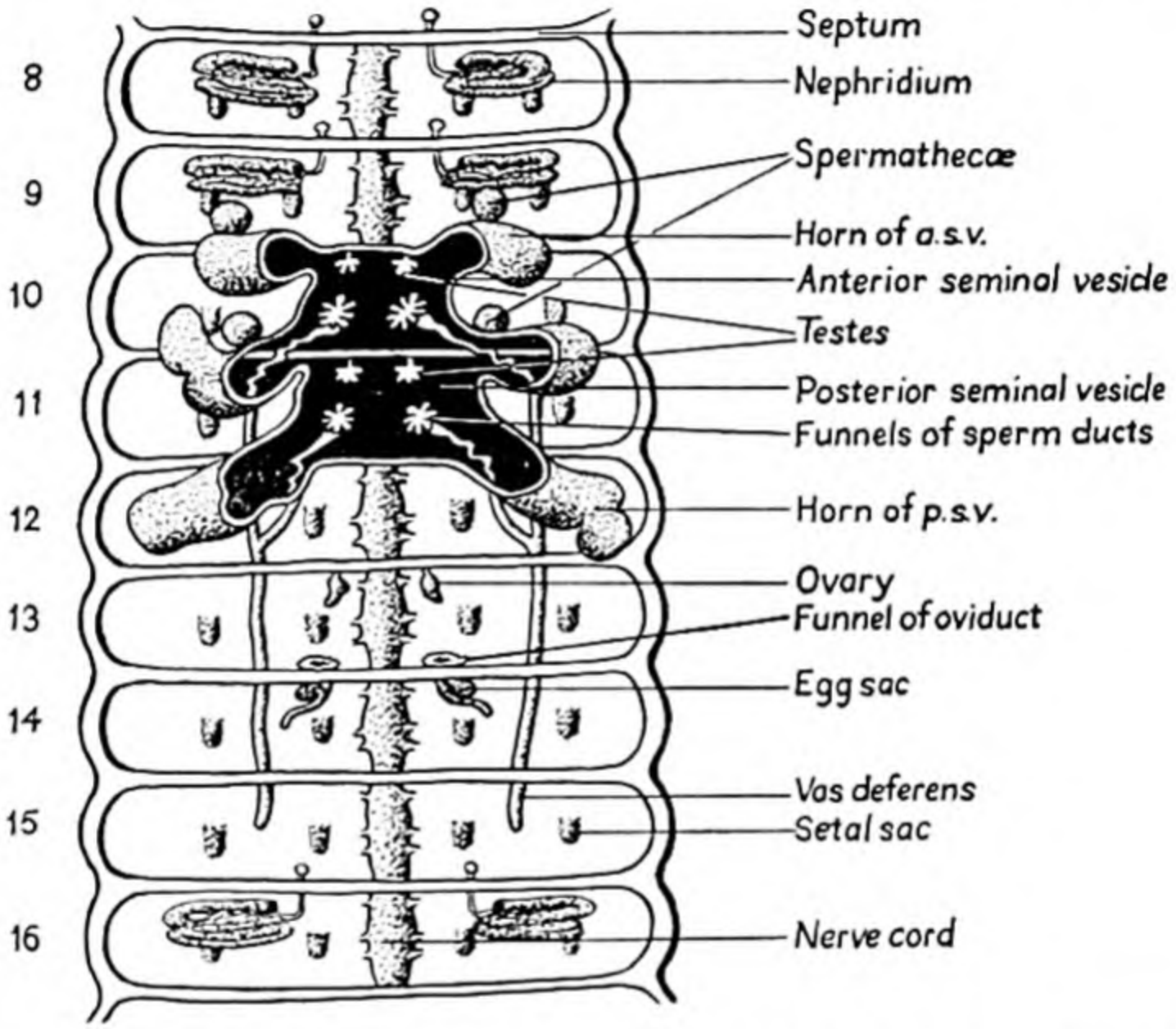


FIG. 42 – *Lumbricus*. The Reproductive Organs. (By courtesy of Professor James Ritchie, from Thomson's *Outlines of Zoology*, 9th edition, O.U.P.)

posteriorly in segment 13, penetrating the septum to reach segment 14, where a swelling occurs to form the **egg sac**, where the eggs are stored. A short oviduct conveys eggs from this sac to the exterior. In addition to these organs for the production and evacuation of eggs, there are present two pairs of blind sacs, opening ventrally into the depressions between segments 9 and 10, and 10 and 11: these are the **spermathecae**. There are two pairs of testes found attached to the anterior septa of segments 10 and 11, and each, as were the ovaries, is a local thickening of coelomic epithelium. The testes are contained within a large, lobed sac, known

as the vesicula seminalis. It is nothing more than a portion of the coelom, specially walled off for this purpose. The anterior portion of the vesicula seminalis, situated in segment 10, is extended into a pair of anterior and a pair of posterior horns, which bulge respectively into the ninth and eleventh segments, whilst the posterior region of segment 11 has a pair of posterior horns projecting into the twelfth segment. The sperm mother-cells, produced in the testes, ripen within these vesiculae seminales. Each sperm mother-cell divides many times to form a large number of small cells surrounding a mass of residual protoplasm. Presently the cells mature into spermatozoa. In all important particulars, including nuclear behaviour, the events leading to the formation of mature spermatozoa resemble those in vertebrates, fully described on page 348. Within each vesicula seminalis is a ciliated funnel, sometimes called a **sperm rosette**, leading into a **vas deferens**, which soon pierces the wall of the vesicula seminalis. The two vasa deferentia on each side unite to open to the exterior by a pore on segment 15.

Although an earthworm is hermaphrodite, cross-fertilisation occurs. Pairing takes place at the surface of the ground under moist, warm conditions, usually in low light intensities, and is prefaced by two worms becoming closely apposed by their ventral surfaces, with their anterior ends pointing in opposite directions. They take up a position such that segments 9 to 11 of each worm lie approximately against the clitellum of the other. There is much secretion of mucus, and the body of each worm becomes invested in a separate mucous envelope from about segment 12 to the clitellum, whilst in each clitellar region there is a common envelope enclosing both copulants. By means of these common envelopes and the stabbing of the elongated ventral chaetae of segment 26 and of the clitellar region of each copulant into the body-wall of the other the two animals remain in this position for several hours, each normally retaining its posterior extremity in the mouth of its burrow. Seminal fluid is now discharged from the male pores on segment 15, from which it passes backwards along the seminal grooves to the clitellum. The seminal grooves are really mis-named, in that at no time are they continuous grooves. They are rather a movable series of pits. The seminal fluid is first collected in a depression in the body-wall in the region of segment 14. Soon this depression here ceases to exist,

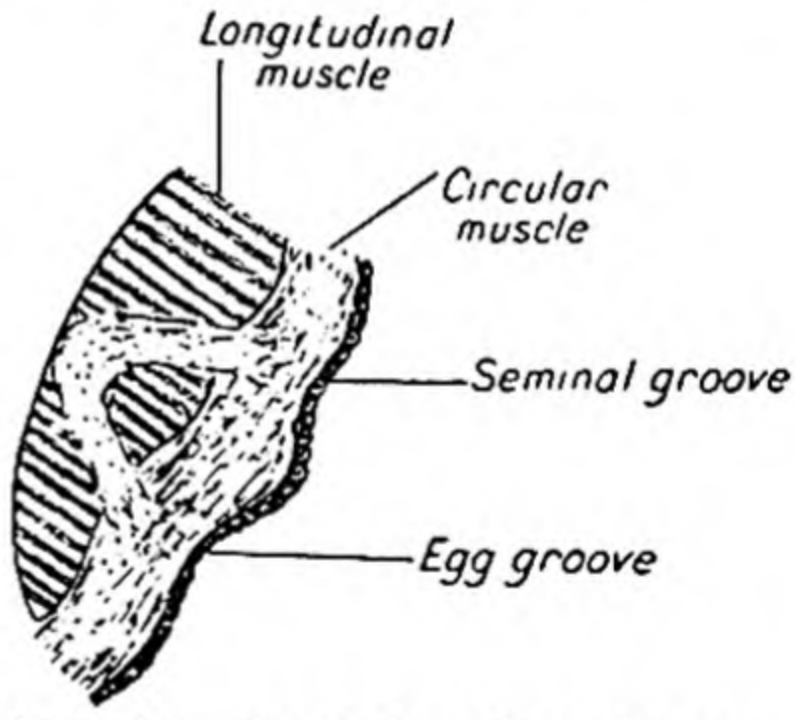


FIG. 43 – Vertical section of body-wall, showing archiform muscles. (After Grove and Newell.)

but appears just behind, so that the seminal fluid is now forced a little nearer to the clitellum. The process is continued until the journey of the seminal fluid is completed. The so-called seminal grooves are therefore really the paths traced by successive seminal pits. The seminal pits are themselves produced by contraction of the special **archiform muscles.** Reference to Fig. 43 will serve to make their disposition clear, and mention of the egg groove, shown in the figure, will be made below. Eventually the seminal fluid collects in depressions in the clitellar region, from which it is passed into the spermathecae of the other worm. After this interchange of spermatozoa the copulants separate, and the same series of events occurs in each.

A slime tube, extending from segments 6 to 40, is now produced, whilst cocoons are secreted at intervals by the clitellum, from which they are separated by albuminous material. Some 8 to 16 eggs are shed from the female pores on segment 14, and these pass along the egg groove in the same manner as did the seminal fluid along the seminal grooves. Once the eggs are enclosed between the clitellum and the cocoon the latter is forced forwards, bearing the eggs in it. As the cocoon passes segments 11 to 9 the foreign spermatozoa are discharged from the spermathecae to fertilise the eggs. The cocoon eventually carries the eggs over the anterior end, and within it development proceeds. Cocoons are deposited about twenty-four hours after copulation, whilst a single supply of spermatozoa may last for up to a year. Only one fertilised egg per cocoon normally completes development, which occurs directly without the intervention of a larval stage, such as occurs in the life-history of most Annelida. A certain degree of regeneration is possible in earthworms. If cut, the posterior segments are more easily regenerated than the anterior, but a new head is formed if no more than fifteen segments are cut off, although the number of regenerated segments is always less than the original. The nerve-cord plays an important part in the regeneration process. Thus if it is cut and pulled out to the side of the anterior region a new head may be formed there.

Coelom

The Platyhelminthes and forms above them (including, therefore, the Annelida) differ from the Coelenterata in one fundamental respect, namely that the body is divisible into three layers. On the outside is the ectoderm, whilst lining the alimentary canal is the endoderm. Between these two there is a mass of tissue, known as the **mesoderm.** In the Platyhelminthes this is nothing more than a network of loosely-packed cells, forming the parenchyma, but in the Annelida it has become much more highly developed. It constitutes the musculature of both the body-wall and the gut-wall, as well as the layer of cells enclosing the gut – i.e. the coelomic epithelium. It is thus clearly divisible into two layers, separated by a cavity known as the coelom, and wherever a coelom occurs it is

always of this nature. In some forms – *e.g.* Arthropoda, of which the cockroach, studied in Chapter 5, is an example – a new type of body-cavity makes its appearance. It is the haemocoel, and will be considered in more detail subsequently (page 73). The true coelom is filled with a coelomic fluid, whilst it is completely enclosed by coelomic epithelium (mesoderm). The functions of the coelom are diverse and important. (1) Since it contains coelomic fluid it supports the viscera (the soft, internal organs of the body) and protects them from mechanical shock while allowing free movement of the gut for peristalsis (page 392). (2) It is the source of the genital (reproductive) products. As already pointed out in the case of *Lumbricus*, these are derived from the coelomic epithelium. (3) It facilitates excretion – the elimination of liquid waste matter. This is particularly obvious in the earthworm, where the nephridia are concerned with the purification of the coelomic fluid. Further, it is from this mesodermal layer that the skeletal tissues of vertebrates are derived. In accordance with the tripartite division of the layers of the body in all forms above the Coelenterata they are collectively classified as the Triploblastica, whilst the Coelenterata are the Diploblastica.

Annelida

In several important respects the structure of the Annelida, as exemplified by *Lumbricus*, shows a marked advance on the condition obtaining in the Platyhelminthes. Thus there is a well-developed coelom, bordered on each side by a layer of mesoderm. The body of the earthworm displays for the first time what is known as **metameric segmentation**. The coelom is divided into compartments by septa, each pierced by the gut, blood-vessels, nerve-cord and a pair of nephridia. In each segment the same organs are repeated, but considerable specialisation occurs at the anterior end, in that the alimentary canal is regionally differentiated, whilst reproductive organs are present. This same phenomenon of segmentation occurs in the majority of higher forms, though it may be masked by the

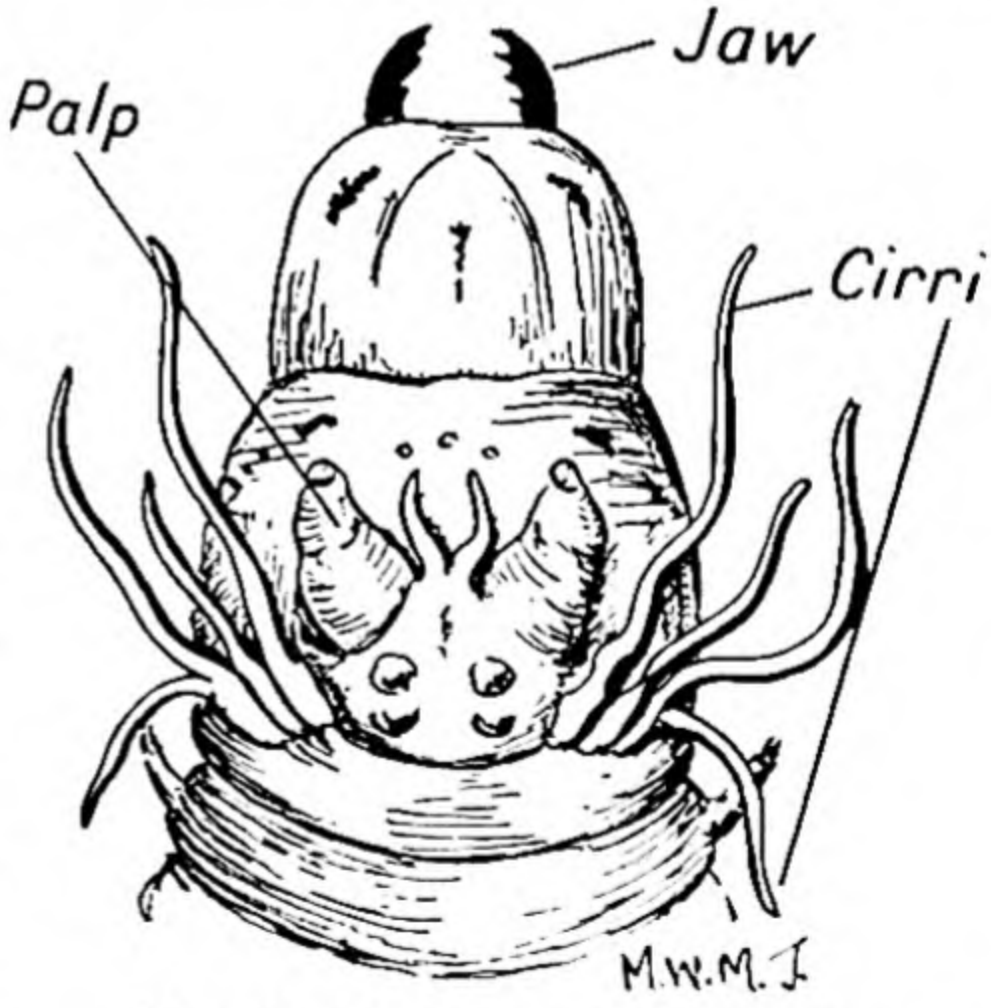


FIG. 44 – *Nereis*. Dorsal view of anterior end, with everted pharynx.

breaking down of the coelomic septa. Thus in vertebrates it is recognisable in the arrangement of vertebrae, nerves and muscles, though the segments are much less alike than in the earthworm. Metameric segmentation is concerned essentially with the coelom, and hence is not to be confused with the division of *Taenia*, for example, into proglottides.

In the earthworm there is demonstrated the beginnings of another phenomenon – **cephalisation**. This signifies the differentiation of a distinct head. In *Lumbricus* it is represented merely by the prostomium, but in other Annelida it has been carried further, several segments being incorporated. In *Nereis*, a marine worm, the prostomium bears a pair of tentacles and a pair of palps, whilst on the segment behind it, known as the peristomium, are four pairs of cirri. The figure on page 65 shows something of the structure of this head region. In higher forms this development has proceeded much further, as is evident, for example, in vertebrates. Differentiation is most marked in respect of the nervous system, for the anterior end of the nerve-cord becomes specialised to form a brain, whilst organs of special sense are localised in the head.

Other advances in the Annelida on the condition in Platyhelminthes are afforded by the presence of a blood-vascular system, whilst the alimentary canal terminates in the form of an anus. The structure of the nervous system, consisting of a pair of supra-pharyngeal ganglia connected with a ventral, ganglionated nerve-cord, is characteristic of all invertebrates above the Platyhelminthes.

PRACTICAL WORK

Dissect several specimens and also draw a transverse section.

Remove a nephridium. Mount in salt solution and examine under the high power of a microscope. Persist with this until you obtain a specimen bearing a nephrostome. Stain and mount this in the manner described for *Hydra*.

Remove an ovary. Stain with paracarmine or borax carmine (page 37).

Make a smear of the contents of a vesicula seminalis as directed on page 24. Examine the various stages of spermatogenesis represented.

CHAPTER 5

Periplaneta

The cockroach is an insect, one of the most important classes of the phylum Arthropoda. It is of considerable biological interest owing to the fact that, in view of its comparative lack of specialisation, it demonstrates very clearly the general characteristics of the Arthropoda, and in particular of the class Insecta. As in all members of the Arthropoda the body is enclosed within an exoskeleton, composed of chitin largely impreg-

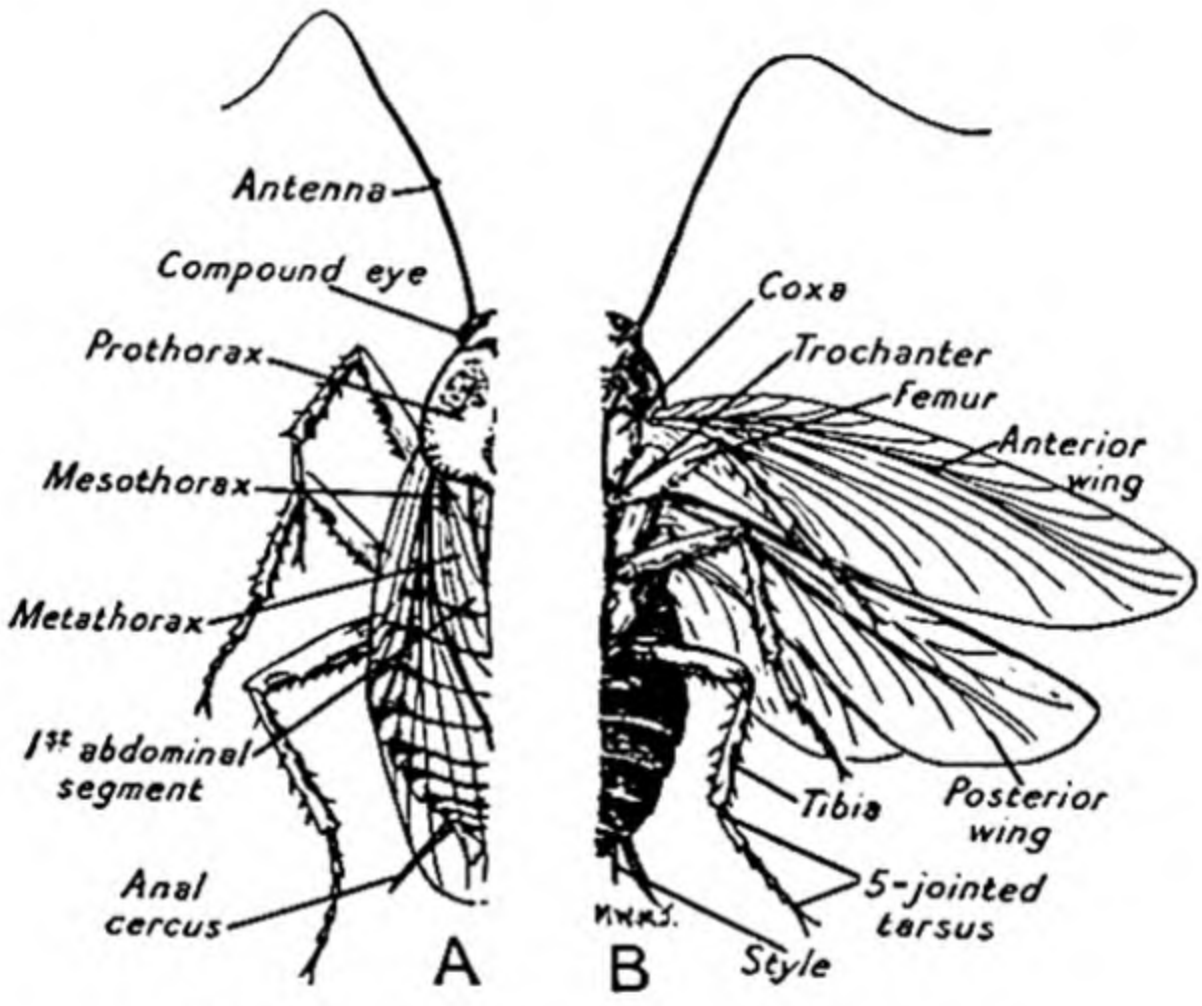


FIG. 45 – *Periplaneta*. External characters.
A., Dorsal view; *B*., Ventral view.

nated with calcium salts, whilst it bears a number of jointed appendages. Typical of primitive insect structure, its body is segmented, and is clearly divisible into three regions, namely head, thorax and abdomen, each of which will be briefly described. In England there are several species of cockroach. The commonest is *Periplaneta* (= *Blatta*) *orientalis*, whilst a much larger variety from America is called *Periplaneta americana*. They exist mostly in buildings offering warmth, protection and suitable food, and are thus common in bakeries. They are described as omnivorous, signifying that they eat any type of available food.

Cuticle

One of the most characteristic features of insects is the possession of a cuticle. In the cockroach this has a total thickness of about 40μ and is divisible into three layers. Covering the surface is a thin, non-chitinous **epicuticle**. It is a very hard and totally impermeable layer, folded at intervals to allow flexibility. On the outside is a covering of protective *cement*, overlying a very thin layer of *wax*, with water-proofing qualities.

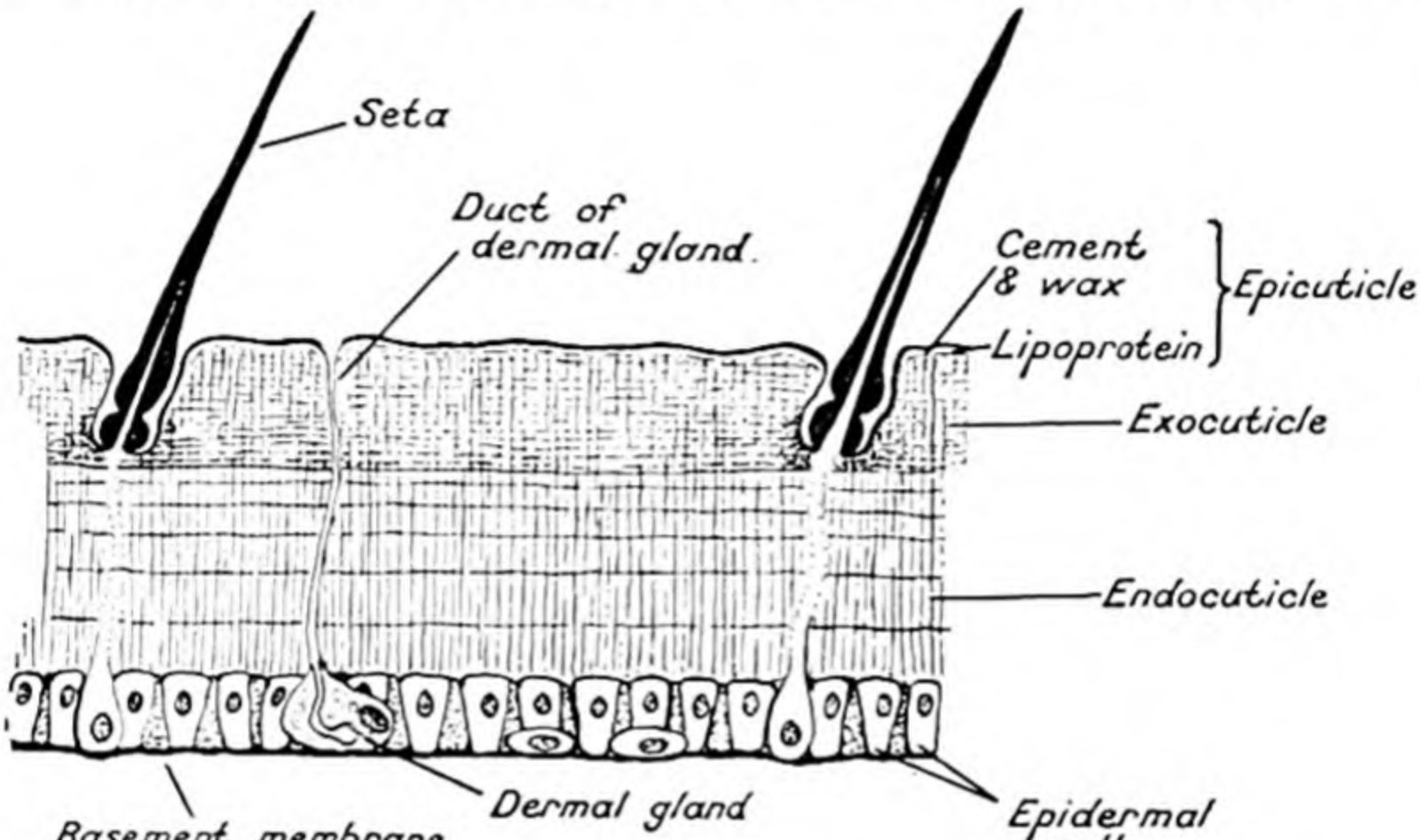


FIG. 46 – *Periplaneta*. Vertical section of cuticle.

The innermost layer consists of a tanned lipoprotein, known as *cuticulin*. Beneath the epicuticle is the **exocuticle**. This consists largely of a layer of tanned protein, known as *sclerotin*, the molecules of which are firmly bound together to form a brown, horny substance. The innermost component of the cuticle is the **endocuticle**. This is the thickest of the three major layers and is composed of minute plates – *micellae* – of *chitin*, which is a nitrogen-containing polysaccharide, in a matrix of a protein, termed *arthropodin*. The whole is often penetrated by vertical channels containing cytoplasm and is relatively flexible.

The entire cuticle is a product of secretion of the cells of the epidermis. At ecdysis (page 79) a moulting fluid is discharged through the newly developing cuticle and this contains enzymes which assist the digestion of the old endocuticle, the products being absorbed into the ectoderm cells through the channels in the new cuticle, the digestion of which is prevented by its own epicuticle. Raising of the blood-pressure within is responsible for the rupture of the old cuticle along predetermined lines, where even the exocuticle is restricted or absent (the endocuticle has already been digested). The new endocuticle is not completed until after ecdysis.

External Characters

The head consists of six segments, indistinguishably fused in the adult. It is a pear-shaped structure, tapering towards the anterior end. Laterally it bears a pair of large **compound eyes**, whilst just median to each is a

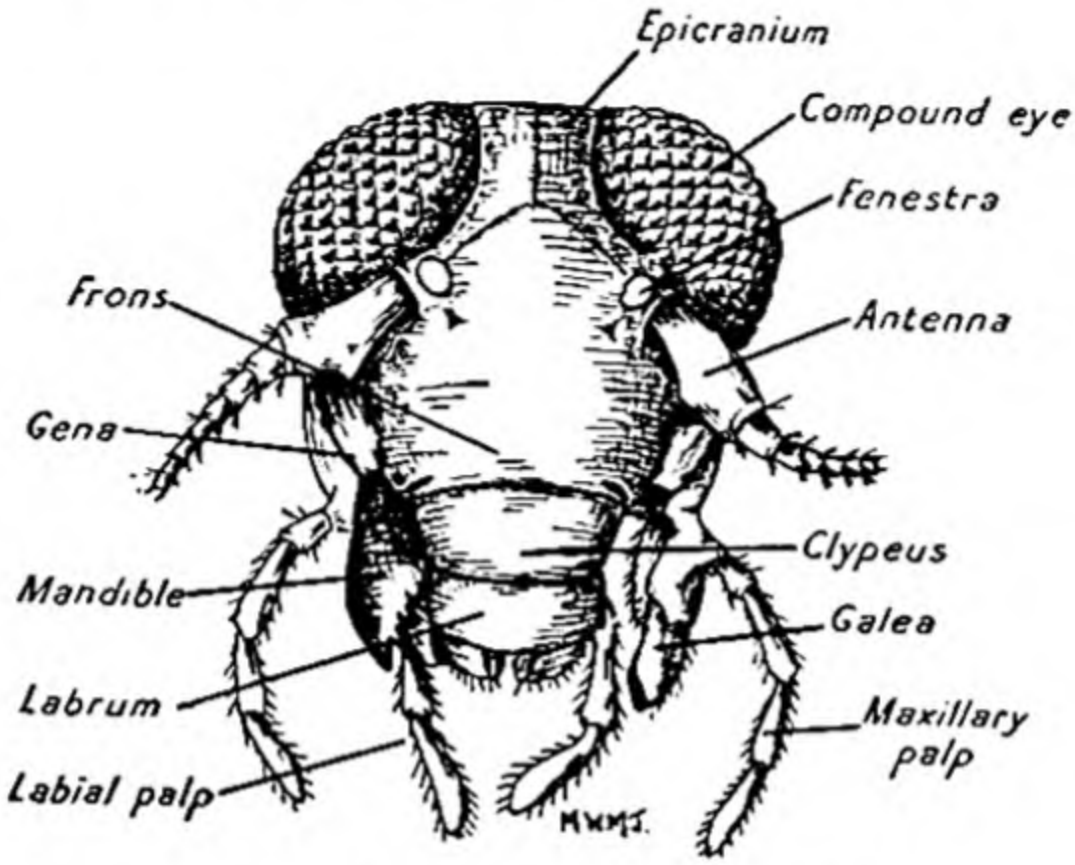


FIG. 47 – *Periplaneta*. The head.

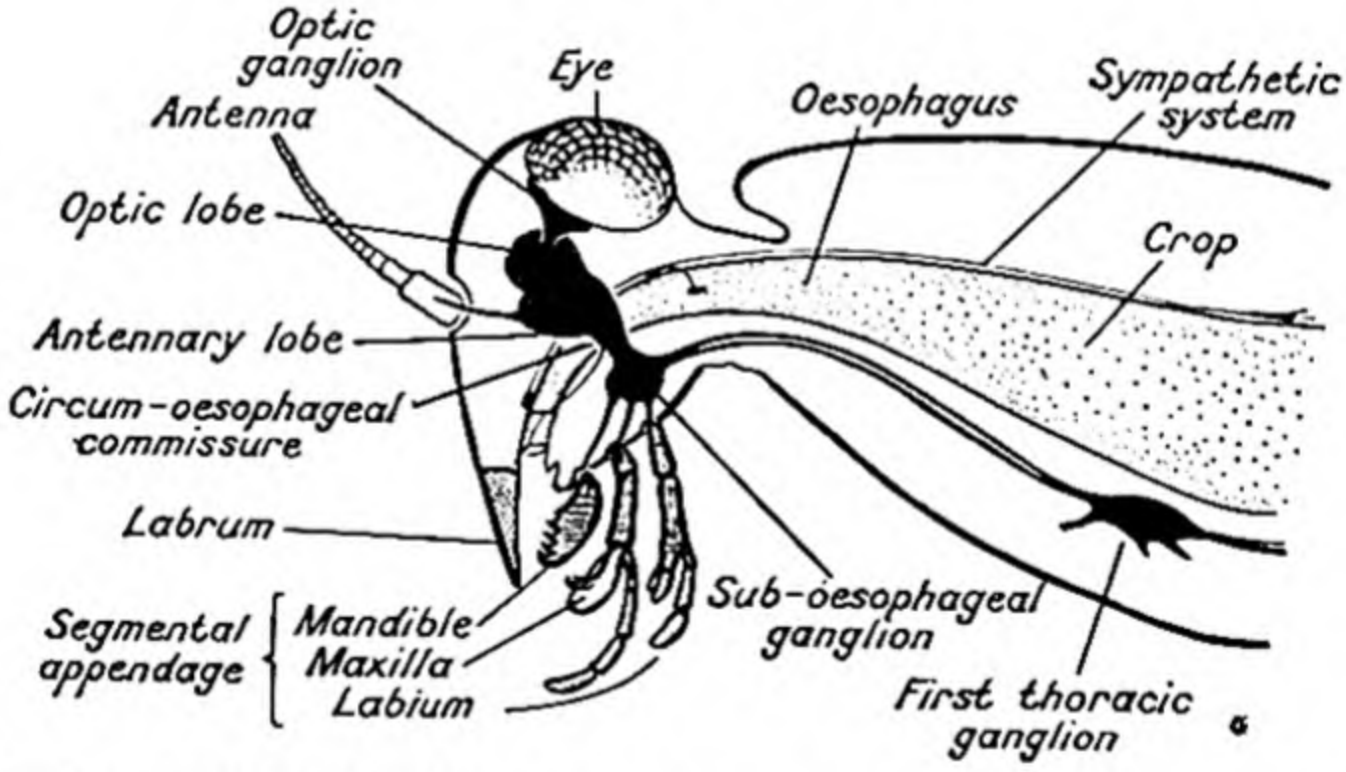


FIG. 48 – *Periplaneta*. Lateral diagram to show the anterior part of the nervous system and the sequence of mouth appendages.

simple eye, or **ocellus**. The skeletal armour of the head is divisible into a number of plates, disposed as shown in Fig. 47. It is characteristic of many segments of members of the phylum Arthropoda that each bears a pair of appendages. In accordance with the composite nature of the head, a number of paired appendages arise, all concerned essentially with the detection, manipulation and preparation of food. Close to each eye arises a long, slender **antenna** (page 76). The apex of the head is

perforated by a mouth, on either side of which is found a **mandible**. This is a small, serrated structure, and the two together are concerned with the cutting and crushing of food. Just posterior to and below each mandible occurs a **maxilla**, consisting of a number of segments, movably

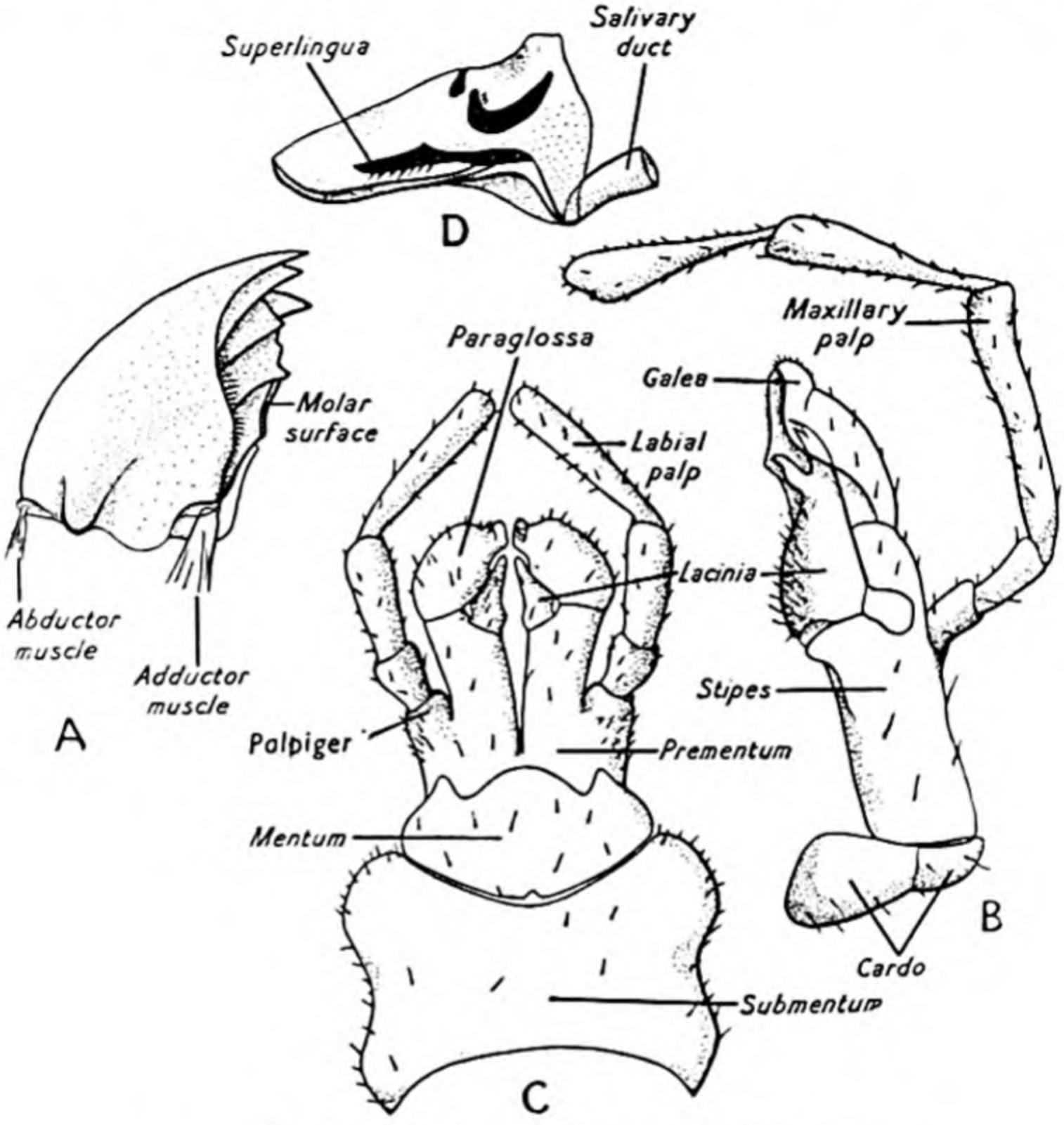


FIG. 49 – *Periplaneta*. The mouth-parts.
A., Mandible; *B*., Maxilla; *C*., Labium; *D*., Hypopharynx.

articulated (Fig. 49B). The maxillary palp is gustatory, whilst the laciniae aid the mandibles in holding the food, since each terminates in a double spine. When at rest the laciniae are covered dorsally by a hood extending inwards; this hood is the galea. The **labium** is a median structure attached just behind the maxillae. It may be regarded as formed from a pair of appendages as a result of partial fusion in the middle line. The extent of this fusion may be judged from Fig. 49C. The labium forms a lower lip, whilst its palps are sensory structures. In this connexion the labrum must be mentioned. It is not of true appendicular nature, but is merely a plate hinged on to the clypeus (Fig. 47). It forms the roof of the buccal

cavity, overlying the mandibles. On its ventral surface occur gustatory organs (chemoreceptors). Attached to the posterior wall of the buccal cavity and projecting freely into it is the **hypopharynx**. This is a tongue-like structure, tapering towards its distal end, though principally in a vertical plane. On either side is a plate, the **superlingua**, whilst dorsal to its base opens the oesophagus. The combined duct of the salivary glands and receptacles discharges its contents into the mouth between the labium and the hypopharynx.

The head is joined to the thorax by a soft, slender neck. The **thorax** is divided into three segments, named antero-posteriorly the **prothorax, mesothorax** and **metathorax**. On each segment is borne a pair of walking limbs. Each limb consists of five principal joints, namely **coxa** (proximal), **trochanter, femur, tibia** and **tarsus** (distal). The last-named is sub-divided into smaller joints, and bears at the end a pair of hooked claws and a porous pad, or **pulvillus**, this latter, as in the house-fly, for example, enabling the insect to attach itself to a smooth surface without slipping. Borne respectively on the mesothorax and metathorax are two pairs of wings. The second pair is membranous and strengthened by a number of nervures, or veins. A wing is at first a flattened, hollow diverticulum of the cuticle, with tracheae extending into it. The tracheae are in turn surrounded by extensions of the haemocoel, containing blood. As upper and lower layers meet and fuse the cavity of the original diverticulum is obliterated. The cuticle thickens about the tracheal-haemocoelic channel, forming the veins of the wing. The front pair of wings, known as **elytra**, is horny and at rest folded lengthwise along the body to cover the hind pair. In *Periplaneta americana* both sexes have wings fully developed, but in *P. orientalis* the wings of the female are much reduced, whilst those of the male do not completely cover the abdomen. The armour of every segment in both the thoracic and abdominal regions consists of a dorsal **tergum** and a ventral **sternum**, joined laterally by a pair of **pleura**. The wings are essentially hollow outgrowths of the body-wall.

The abdomen consists of eleven segments, slightly telescoped posteriorly so that the eighth and ninth are scarcely visible. The tergum of the tenth segment is continued into a deeply-notched process, beneath which two jointed **cerci anales**, the appendages of the eleventh segment, are attached. The corresponding sternum bears a pair of **podical plates**, between which lies the anus. As well as the cerci of the eleventh segment, abdominal appendages are probably represented on the eighth and ninth segments by the **gonapophyses**, which surround the genital aperture, itself situated just below the anus. In the male a pair of short styles projects from the ninth segment, whilst in the female the sternum of the seventh segment is modified into a depression, forming the floor of the genital pouch.

Alimentary System

The gut of the cockroach is a tube leading from mouth to anus. It is peculiar in that the greater part of it is lined with ectoderm, since it is formed by a process of invagination from the mouth and anus. This ectodermal part of the gut is, therefore, lined with cuticle. There is a short mid-gut, or **mesenteron**, of true endoderm, the part of the alimen-

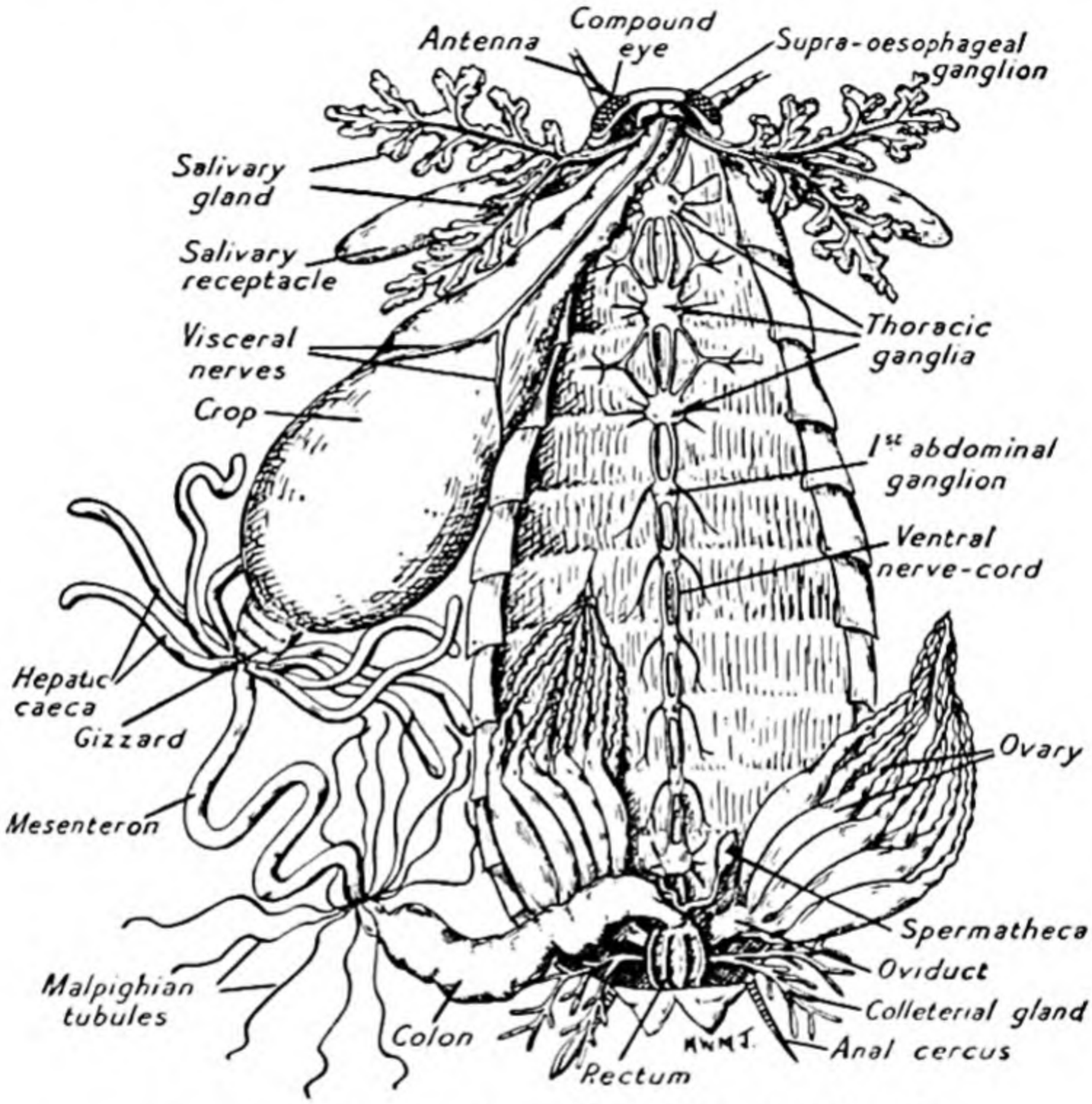


FIG. 50 – *Periplaneta*. General dissection of the female.

tary canal anterior to this being known as the **stomodaeum** and that posterior as the **proctodaeum**. Thus the mouth leads into a buccal cavity, the floor of which receives the duct of the **salivary glands**. Of these there is a pair on either side of the oesophagus. Between the two members of each pair lies a **salivary receptacle**. A separate duct arises from each gland. The two ducts on each side quickly unite and soon join the duct from the other side. This combined duct receives a further tube formed by the union of the ducts from the receptacles. Finally this composite duct discharges into the floor of the buccal cavity. The mouth is connected by a

narrow oesophagus with an expanded crop, which in turn communicates with a gizzard. The walls of the gizzard are specially cuticularised to form a number of horny teeth, whilst posteriorly a number of bristles prevent too large particles from passing through unmasticated. From the gizzard the food passes into the endodermal mesenteron, at the beginning of which are set seven or eight club-shaped diverticula, known as **hepatic caeca**. At the junction of the mesenteron with the proctodaeum is a mass of fine **Malpighian tubules**, of excretory function. The proctodaeum is differentiated into a narrow **ileum**, followed by a **colon**, which communicates with the anus by a wide **rectum**.

Saliva, containing amylase, is ejected on to the food, which is thus moistened. The greater part of the digestive process occurs in the crop, where not only does the salivary amylase assist, but also the full complement of mesenteric enzymes, secreted by the lining cells of that part of the gut and passed forward. This latter group of enzymes includes amylase, maltase, invertase, tryptase, peptidase and lipase. In addition, some digestion in the crop is accomplished by any yeasts and Bacteria which may enter with the food. Absorption occurs in the mesenteron and hepatic caeca. The endothelium (page 329) of the mesenteron is protected by a thin *peritrophic membrane*, permeable both to digestive juices and also to the dissolved products of digestion. Water is absorbed in the hind-gut and solid faeces are discharged through the anus.

Vascular System

The blood-vascular system of the cockroach is but poorly developed. It is peculiar in the total absence of capillaries, the blood being circulated through series of ill-defined spaces, which together constitute the body-cavity of the cockroach. Such a body-cavity is appropriately termed a **haemocoel**, and the true coelom is confined in this animal to the cavities of the gonads: there are thus no coelomic excretory organs present and all the tissues of the body are directly bathed in blood. Within this haemocoel a white substance, known as *fat body*, occurs and it is believed to play some part in the storage of excesses, including albumen, fat and glycogen. It is also involved in the excretory process and its frequent greenish colour is due to the presence of urates.

The haemocoel is divided by two incomplete, horizontal diaphragms into three spaces, or **sinuses**, known respectively as the *pericardial sinus* (dorsal), the *visceral sinus* (central) and the *perineural sinus* (ventral). Inserted into the dorsal diaphragm and originating from the terga are twelve pairs of fan-shaped *alary muscles*. Situated in the pericardial sinus is a longitudinal **heart**, incompletely divided into thirteen segmental chambers which communicate with each other through apertures fitted with *ventricular valves*. Each chamber further communicates with the pericardial sinus via a pair of lateral slits, or **ostia**, each guarded by an *auricular valve*. Extending forwards from the most anterior chamber of

the heart is a narrow **aorta**.

When the heart contracts, from behind forwards, blood is expelled through the aorta into the head sinus and thence to the visceral and

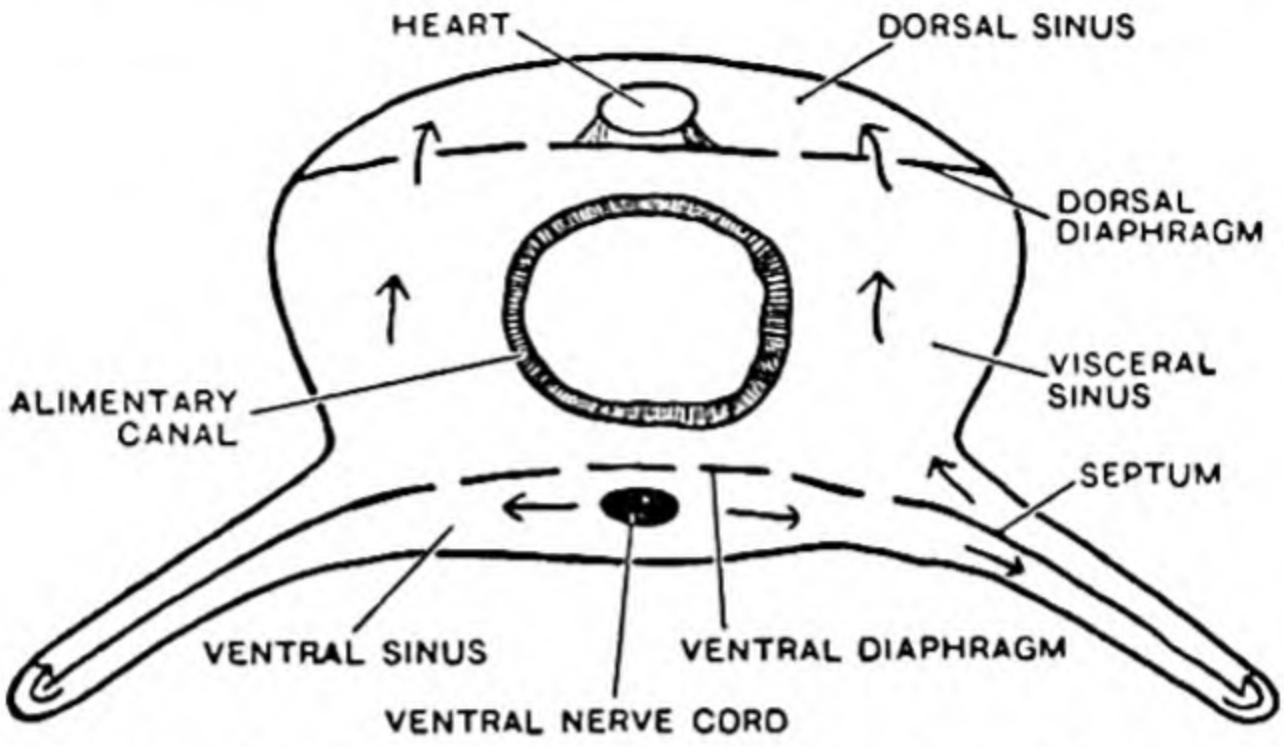


FIG. 51. – Transverse section through the thorax of a cockroach to show the positions of the diaphragms and direction of the blood flow. (From an article by Chapman Pincher in *School Science Review*, Vol. XXX, No. 110. John Murray.)

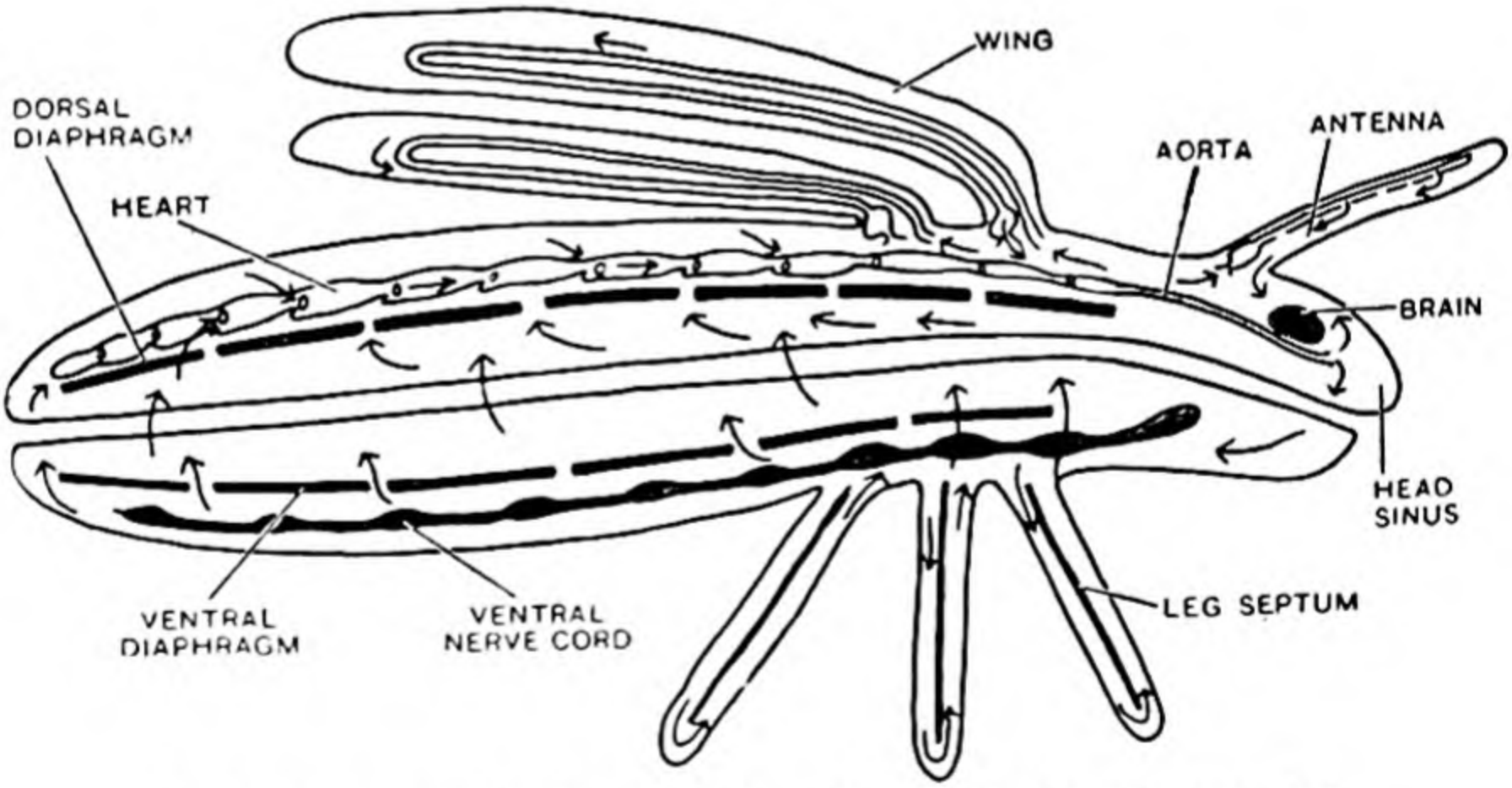


FIG. 52. – Longitudinal section of a cockroach to show the general circulatory system. (From an article by Chapman Pincher in *S.S.R.*, Vol. XXX, No. 110. John Murray.)

perineural sinuses. In consequence, blood already present in these sinuses is forced backwards and there is a general movement dorsally around the edges of the diaphragms and through the perforations in them. When the alary muscles contract the pericardial sinus increases in volume, thus

further facilitating the dorsal movement of the blood, which is able to enter the heart via the ostia, the auricular valves being open and the ventriculars closed. When the heart contracts the ventricular valves are forced open and the auriculars caused to close. The contraction of the heart is rhythmical, but the speed of contraction is under nervous control.

A definite circulation is maintained in the appendages, each antenna and wing being served by special pulsating organs in the head and thorax respectively. Each leg is provided with a median septum, blood entering along the internal border and leaving along the external border.

The blood itself consists of a plasma containing colourless corpuscles (*leucocytes*). The latter are variable in number, shape and size. An average number is 30,000 per cu. mm. and an average size 0·015μ.

Respiratory System

The cockroach has a well-developed respiratory system of branching tubes, or **tracheae**. These open on to the lateral surface by a number of inter-segmental orifices, known as **stigmata**, or spiracles, the first pair occurring between the pro- and meso-thorax, and the remainder between every two succeeding segments until in all there are ten pairs. The whole tracheal system is of ectodermal origin and is lined with cuticle, which becomes considerably folded, giving the impression that the tubes are spirally thickened. Passing inwards from the stigmata, successive branches become progressively narrower, when suddenly, at a width of about 2μ, each bears a multiple group of tracheoles, of diameter 0.6 to 0.8μ. These penetrate intimately into the tissues and gaseous exchange occurs through their non-cuticularised walls. Every tracheole, is, in fact, one large, hollow cell, with a single nucleus lying in the wall. When the insect is at rest the stigmata are normally closed. During periods of activity the main tracheae are ventilated as a result of the dorso-ventral movements of the trunk, the tracheae being first compressed and then expanding again as a result of the elasticity of their walls. The condition of the thoracic stigmata, where a complicated opening and

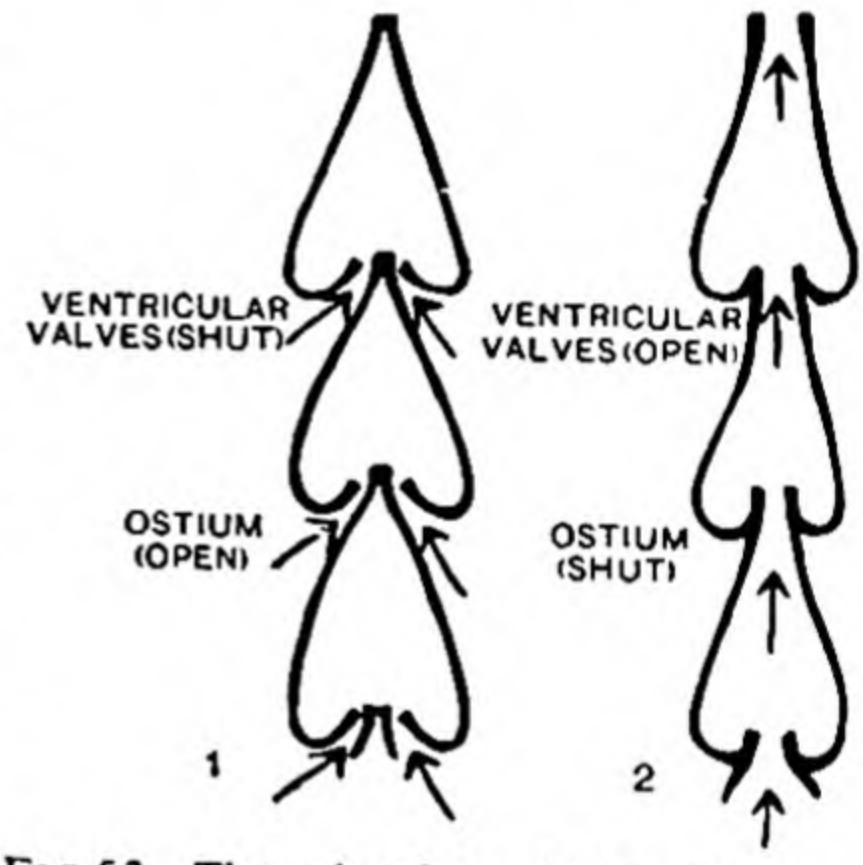


FIG. 53.–Three chambers of the cockroach heart showing: (1) the condition of the valves as blood enters the heart from the dorsal sinus, and (2) their position as the heart contracts, driving the contained blood forwards. (From an article by Chapman Pincher in *S.S.R.*, Vol. XXX, No. 110. John Murray.)

closing mechanism exists, is under the control of nerves from various ganglia and a high concentration of carbon dioxide in the tissues provides a stimulus for their opening. The abdominal stigmata are permanently open. Once air is in the tracheae its passage into the tracheoles is achieved by simple diffusion. The anastomosis of tracheoles means that any organ can acquire oxygen from a wide radius during periods of great activity. It is usual for fluids to be present in the terminal tracheoles except during such periods, when the raising of the osmotic pressure of the tissues as a result of the accumulation of metabolic waste results in their withdrawal. Thus oxygen may penetrate more deeply into the working organ.

It is interesting to speculate to what extent the tracheal respiratory system has limited the size of the bodies and 'brains' of insects. With some system better adapted for the transport of respiratory gases over greater distances, insects could well have become larger and more intelligent. Man's supremacy may well, in fact, have been challenged, if, indeed, he had ever evolved at all.

Excretory System

The Malpighian tubules are regarded as the excretory organs of insects, though there seems some doubt as to how far this function is exercised in the cockroach. The distal portions of the tubules actively extract urates from the haemocoel. In the more proximal regions, where brush-border cells retard the speed of liquid flow, uric acid is precipitated under the influence of carbon dioxide, the bicarbonates thus formed being resorbed, together with water, into the blood, whilst the uric acid is passed into the hind-gut for elimination through the anus. As already noted (page 73) the fat body may be at least a temporary storage centre for urates.

Nervous System

Two **supra-oesophageal ganglia**, supplying the eyes and antennae, are joined by two peri-oesophageal connectives with a sub-oesophageal ganglion, from which runs a double, ventral nerve-cord. This becomes enlarged in each of the three thoracic and the first six abdominal segments to form a ganglion. There is a visceral nervous system passing from the peri-oesophageal connectives to supply the alimentary canal, and its chief ganglion lies dorsal to the crop. The sense organs include a pair of compound eyes, a pair of antennae, said to be olfactory and gustatory (chemoreceptors), scattered sensillae in the palps and legs to detect mechanical strains in the chitin of the exoskeleton (proprioceptors), together with the tactile anal cerci.

The structure of a **compound eye** is peculiar in that it consists essentially of a large number of simple eyes, or **ommatidia**. The whole eye is covered by a transparent cuticle, known as the **cornea** and subdivided into facets,

each facet corresponding to an ommatidium, which is itself an ectodermal structure. It consists of a number of pigmented nerve-cells at the base, forming the **retinula**. The nerve-fibres from these cells run into the supra-oesophageal ganglia, and the cells of each ommatidium surround a refractive body, termed a **rhabdome**, which they secrete. Running forward from the rhabdome are four very much elongated cells known

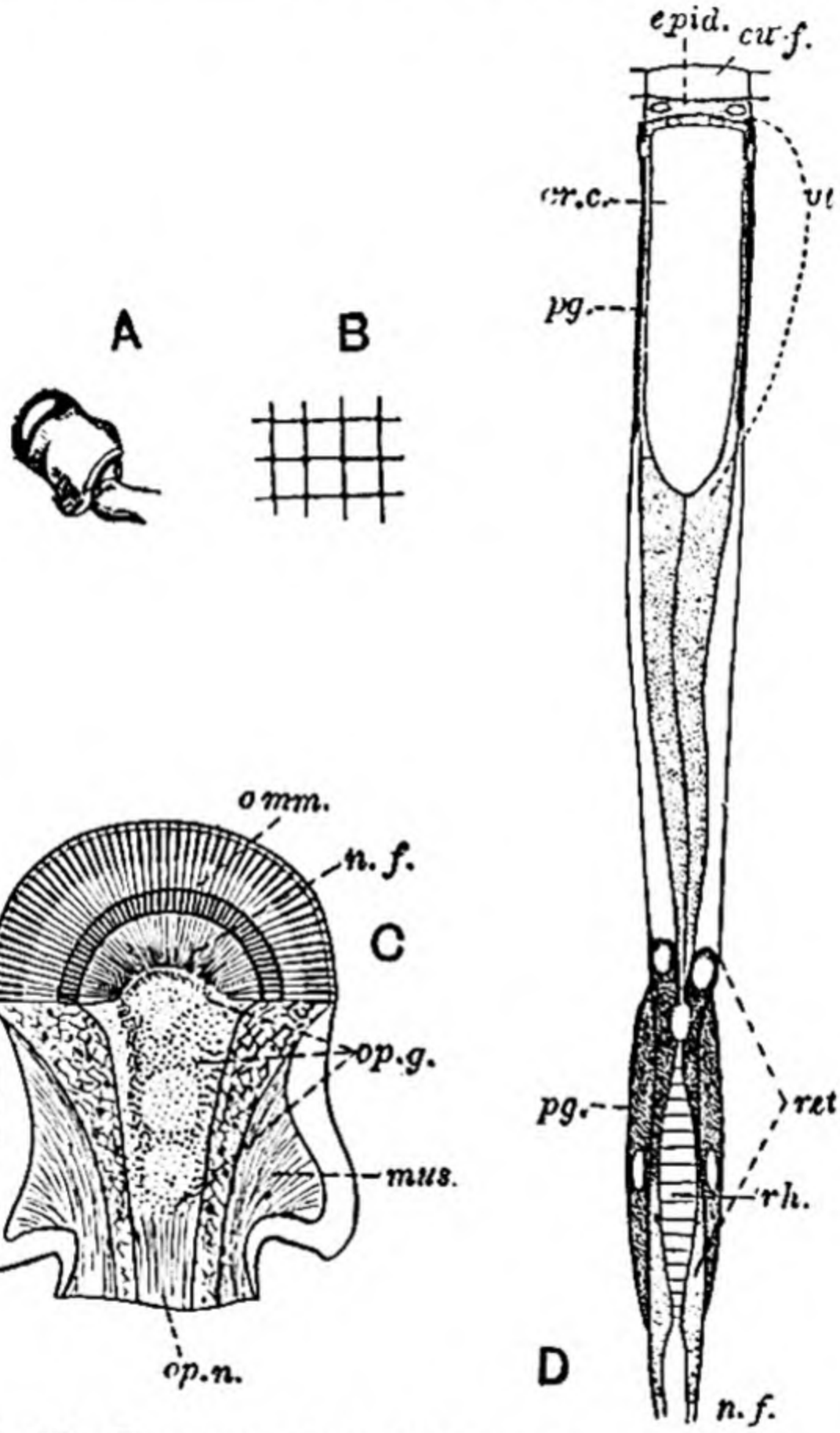


FIG. 54 – The Compound Eye of Arthropoda. (From 'Manual of Zoology', by L. A. Borradaile. O.U.P.)

A., The left eye removed; *B.*, a portion of the cornea magnified to show the facets; *C.*, a longitudinal section of the eye under low power; *D.*, a single ommatidium highly magnified.

cr.c., crystalline cone; *cu.f.*, cuticular facet; *epid.*, epidermis; *mus.*, muscles which move the eye; *n.f.*, nerve fibres; *omm.*, ommatidia; *op.g.*, optic ganglion; *op.n.*, optic nerve; *p.g.*, outer and inner pigment cells; *ret.*, retinula cells; *rh.*, rhabdome; *vt.*, vitrellae.

as **vitrellae**, whose function is to produce and enclose a more superficial refractory body, called the **crystalline cone**. Separating the crystalline cone from its facet of the cornea are four ectoderm cells. Thus the functions of the various cells constituting an ommatidium are sensitive (the retinulae), secretory (the vitrellae) or supporting. The crystalline cone and the rhabdome are obviously concerned with focusing. The ommatidia are separated from each other by pigment cells. In bright light this pigment is widely dispersed, so that the ommatidia are individually isolated. This means that every ommatidium will form a completely independent image from rays of light entering along its main vertical axis. Such a mosaic is termed an apposition image. In diffuse light the pigment cells contract and a more unified image is apparently formed, for light may be received by every ommatidium even if it is entering somewhat obliquely. It must be imagined that, whichever type of image is formed, impulses will be conveyed from the ommatidia to the 'brain' to be translated in such a way that only one impression is registered and appropriate responses elicited.

Reproductive System

The sexes are separate in the cockroach. There is a pair of ovaries in the hind part of the abdomen of the female, and each consists of eight tubes which taper to points at their free ends. At their posterior ends they give rise to tubes which join, and the conjoined tubes of the two sides unite to form a median oviduct, opening on to the sternum of the eighth abdominal segment. Between the sterna of the eighth and ninth abdominal segments opens a **spermathecal pore**, within which the spermatheca bifurcates, but only one branch completes development, the other withering. On the ninth abdominal sternum are two openings from the pair of **colleterial glands**, which function to produce material for the formation of egg-cases. In the male paired testes occur. From them spermatozoa are conveyed away along sperm-ducts, each of which becomes enlarged to form a vesicula seminalis. Each of these becomes so much subdivided that the two, lying close together in the middle line, are known as the **mushroom-shaped gland**. Here spermatozoa are possibly stored, but more

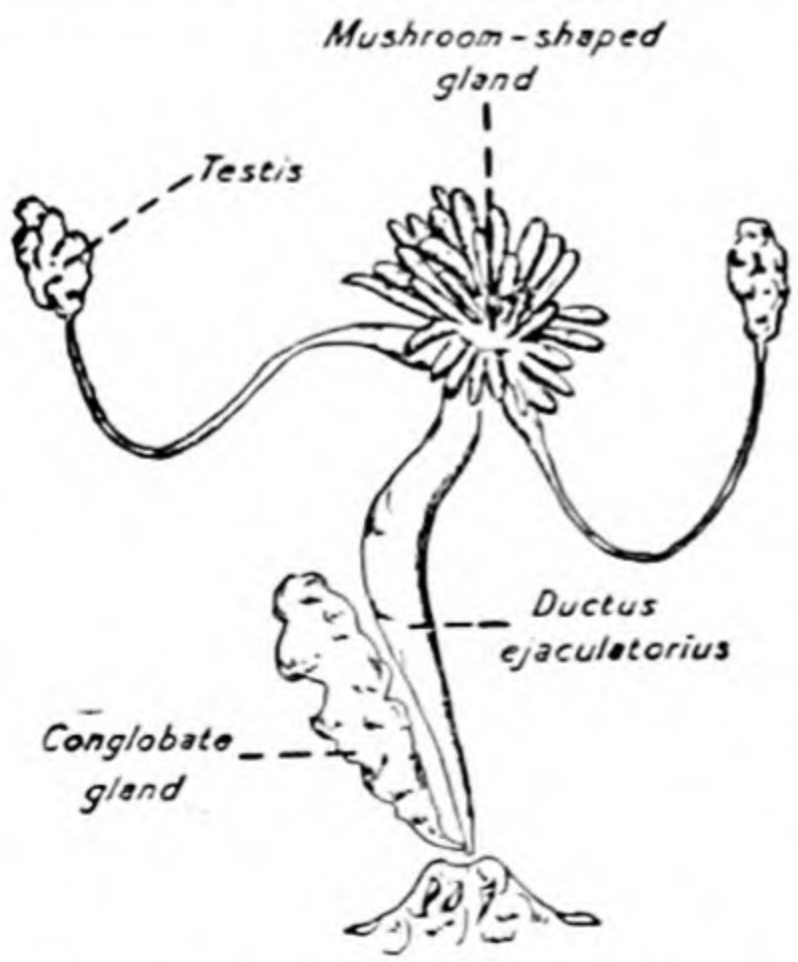


FIG. 55 – *Periplaneta*. Male reproductive system.

likely are nourished by a special fluid secreted for that purpose. They reach the exterior through a muscular **ductus ejaculatorius**, into which both seminal vesicles discharge. This opens to the exterior by a median pore between the sterna of the ninth and tenth abdominal segments. Just ventral to this duct lies the **conglobate gland**, of doubtful function, opening confluent with the male genital pore. At copulation sperms are discharged into the spermatheca, and later fertilisation occurs. Breeding occurs throughout the year. Eggs are liberated singly from each ovary in turn and sixteen fertilised eggs are enclosed in two rows in an oötheca, formed by the colleterial glands. The capsule is retained in the genital pouch for some time and development commences at once. Later the capsule is deposited in a sheltered crevice, near a supply of suitable food, when development is completed, the whole normally occupying about a year. There is no larval stage in the life-history of the cockroach and the hatched insect – virtually in adult form – is termed a **nymph** (see below). Concerned in the deposition of eggs are six gonapophyses in the region of the genital apertures. Morphologically these may represent modified abdominal appendages.

Conclusion

Having acquired a knowledge of the anatomy and physiology of the cockroach as a typical insect, the peculiarities associated with its structural organisation may be investigated. Most important in this connexion is the exoskeleton, both in adult life and during development. An exoskeleton affords efficient protection, but provides no means of attachment for muscles. Accordingly an endoskeleton is developed, in addition to the exoskeleton. It is formed as a result of the invagination of the integument to form stiff rods, consequently so important in all forms of muscular activity. These rods arise in all three regions of the body, whilst in each region they occupy dorsal, ventral and lateral positions, being developed respectively from the terga, sterna and pleura. Such a skeleton is distinguished from the true mesodermal skeleton of vertebrates by the term **endophragmal**.

The presence of a chitinous exoskeleton must necessarily exert a considerable influence upon the course of organic growth. This latter must always be prefaced by a shedding of the entire integument, a process known as **ecdysis**. Not only are the skeletal coverings of the segments cast off, but with them is included the lining of the stomodaeum, proctodaeum and tracheae. A new cuticle is formed by the activities of the hypodermal cells, prior to the shedding of the old, so that at no time is the soft body-wall left unprotected (see page 68).

Stages in insect development are both interesting and important. When the egg is hatched the organism thus liberated may be termed either a nymph or a larva. A **nymph** has reached an advanced stage of development and, on leaving the egg, closely resembles the adult (imago)

except in the incomplete development of genitalia and wings. A **larva,** on the other hand, is at an early developmental phase, differing markedly from the adult, principally in the form of the mouth-parts, whilst compound eyes are as yet wanting or, if present, are non-functional. The hatched grub of a cockroach affords an example of a nymph, whilst the butterfly caterpillar is a larva. The nymph or larva grows by means of a series of ecdyses, and the intervals between successive ecydses are termed **stadia**. The form assumed during a stadium is an **instar**. Thus, for example, on emergence from the egg the caterpillar is the first larval instar. In those life-histories where a larva appears this is followed by another stage – the **pupa**. The pupa is that instar whose larval organs become remoulded to fulfil the requirements of the adult. It appears as a result of the extension of the normally short period of inactivity which frequently precedes an ecdysis. This series of changes of organs from larval to adult form is known as **metamorphosis**. The degree to which it occurs varies from almost complete absence to the full expression found, for example, in Lepidoptera (butterflies and moths).

PRACTICAL WORK

Examine and draw a male and female cockroach with a view to determining the external characters.

Dissect a large cockroach according to instructions given in textbooks of practical zoology. For this purpose the animal is best fixed in position by being placed in molten wax with the dorsal surface protruding. Take care that the upper surface of the head is also clear of wax, since it will have to be opened for the dissection of the cerebral ganglia.

Remove the salivary glands and their receptacles and stain them in the manner described for *Hydra*.

Cut off the head at the neck and boil in caustic soda solution. Hold the head from its posterior end in stout forceps and carefully remove each mouth-part in turn, taking a firm grip of it *at its base* with fine forceps. As removed place them into 70% alcohol and after a short time into two successive lots of absolute, allowing ten minutes in each. From this transfer to two lots of xylene and mount in Canada balsam, arranging them as in Fig. 49. They should be grouped quite close together on the slide, since the lowering of the cover-slip into position will force them apart.

Remove a portion of a trachea from a dissected specimen and mount in glycerol. Examine under a microscope, noting particularly the spiral thickening.

CHAPTER 6

Scyliorhinus

Scyliorhinus, the dogfish, is the first of three types to be studied as examples of the phylum Chordata. Members of this phylum are separated from the Invertebrata by several diagnostic characters, though they possess certain features in common. Thus both vertebrates (Craniata) and the higher invertebrates are coelomate Triploblastica, usually bilaterally symmetrical, and their bodies are often segmented. But in other respects a vertebrate differs typically from an invertebrate. Thus it possesses a **notochord**. This is an elastic rod, functioning as a skeletal support and primitively extending throughout the length of the animal. In the vast majority of forms it becomes more or less completely invaded and replaced by cartilage or bone as development proceeds, the vertebral column, or backbone, taking its place. Respiration is primitively effected by pharyngeal **gill-slits**. In higher vertebrates these structures become very largely suppressed, but rudiments still persist in the form, for example, of the Eustachian tube. Blood is maintained in motion in vertebrates by a ventral heart, through which blood flows forwards. It will be recalled that blood flows forwards in the dorsal vessel of the earthworm, for instance. The main skeleton of a vertebrate is internal, whereas an exoskeleton is common in invertebrates, especially in the Arthropoda. It is true that an endophragmal skeleton is developed in Arthropoda by the ingrowth of stiff, chitinous processes from the exoskeleton, serving for the attachment of muscles, but this is in no way homologous (page 594) with the endoskeleton of vertebrates. In the invertebrates appendages, where present, are typically arranged one pair per segment, but the appendages of vertebrates arise each from several segments. In vertebrates the nerve-cord is tubular and dorsal in position, whilst that of invertebrates is solid and ventral. The nerves themselves in vertebrates are clearly divided into afferent and efferent fibres before entering the central nervous system. Only rudimentary attempts at this separation are found in invertebrates, as mentioned in the case of the earthworm on page 61. These diagnostic features of the Craniata should be noticed as the dogfish and two succeeding types are described.

External Characters

The dogfish, actually a small shark, occurs around the British coast, where the commonest species, *Scyliorhinus canicula*, or the lesser-spotted dogfish, preys on almost any form of animal food, though living princi-

pally on Crustacea. It derives its name from the fact that hunting is done in packs, and is largely facilitated by a keen sense of smell. The body is some two feet in length, and a distinct head and tail may be discerned. The head, wider in the female than in the male, is, in both sexes, compressed dorso-ventrally, and on the ventral surface near the front end is a crescentic mouth. Just in front of the mouth is a pair of nostrils, whilst situated laterally on the head is a pair of slit-like eyes. On each side of the body, just behind the eyes, are six small openings, leading into tubes communicating with the pharynx (see later). These are the **gill-slits**. The first one is smaller than the remainder and is situated more dorsally, lying immediately behind the eye: it is known as the **spiracle**. The trunk, especially posteriorly, is laterally compressed, and bears a number of fins. There is a pair of **pectoral fins** arising just behind the head.

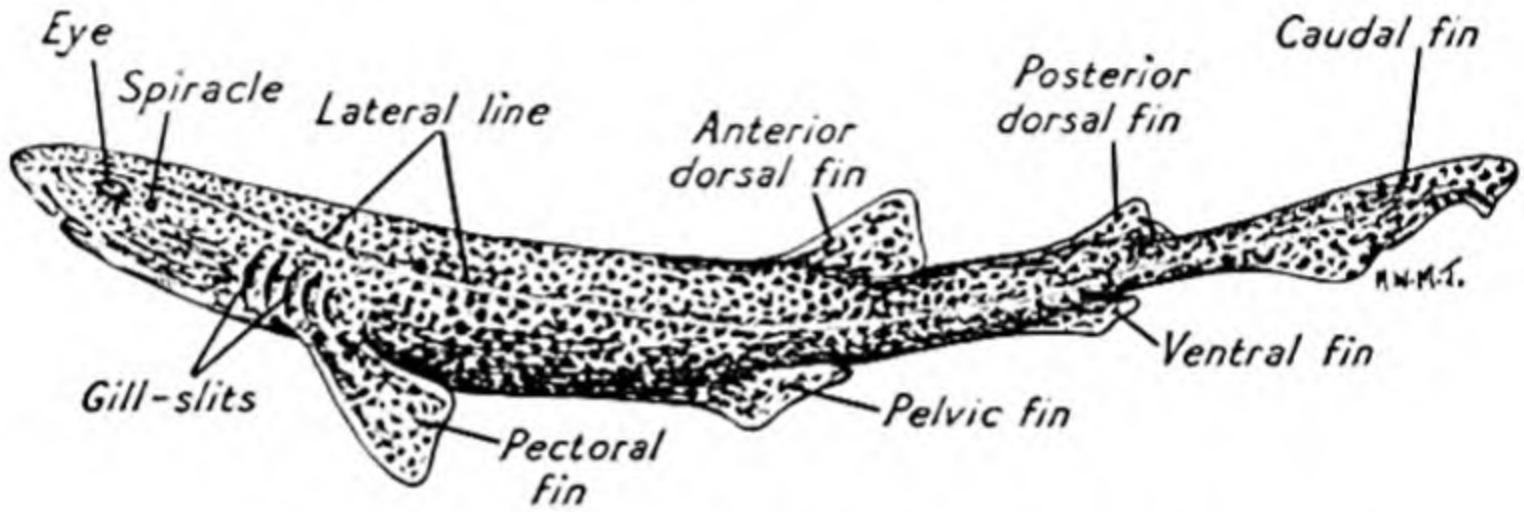


FIG. 56 – *Scyliorhinus*. The body from the left side.

They are ventro-lateral in position and correspond to the fore-limbs of the Tetrapoda – the four classes of Craniata above the fish, namely Amphibia, reptiles, birds and mammals. A pair of **pelvic fins** lies behind the pectorals, arising close to the mid-ventral line. They are smaller than the pectoral fins, and in the male their inner edges are fused proximally, whilst there projects backwards from the ventral surface of each a grooved rod, known as a **clasper**. This is the only means of external distinction between male and female. As well as the paired fins already described there is present also a number of median fins. Arising about one-third of the length of the animal from the posterior end is a small **anterior dorsal fin**, whilst a short distance behind this is the **posterior dorsal fin**. Between the positions occupied by these two fins, but in the mid-ventral line, arises a further small fin, known in consequence as the **ventral fin**. The tail is enveloped in the vertical plane by a **caudal fin**, of which the ventral lobe is slightly larger than the dorsal. The **cloaca** is situated in the mid-ventral line, between the pelvic fins, whilst on either side of it is a minute **abdominal pore**, communicating between the coelom and the exterior. The whole surface is covered with sharp spines, known as **denticles**, or placoid scales. Each consists of a mass of **dentine**, produced by the dermis of the skin, and is covered with a cap of **enamel**,

secreted by the ectoderm. As will be seen later this is very like the structure of a tooth of higher forms. In fact, in the dogfish similar but slightly enlarged scales are arranged around the margin of the jaws to function as teeth. These are larger and more widely dispersed in the male than in the female. Running along either side of the body may be distinguished a faint line. This is the **lateral line**, which will be dealt with in more detail later (page 103).

Skin and Scales

As in the remainder of the Craniata the skin is divisible into two layers. The outer layer is derived during development from a layer of cells known as the ectoderm (page 502), and constitutes the **epidermis**. Beneath it is a layer of mesodermal origin, forming the **dermis**. The

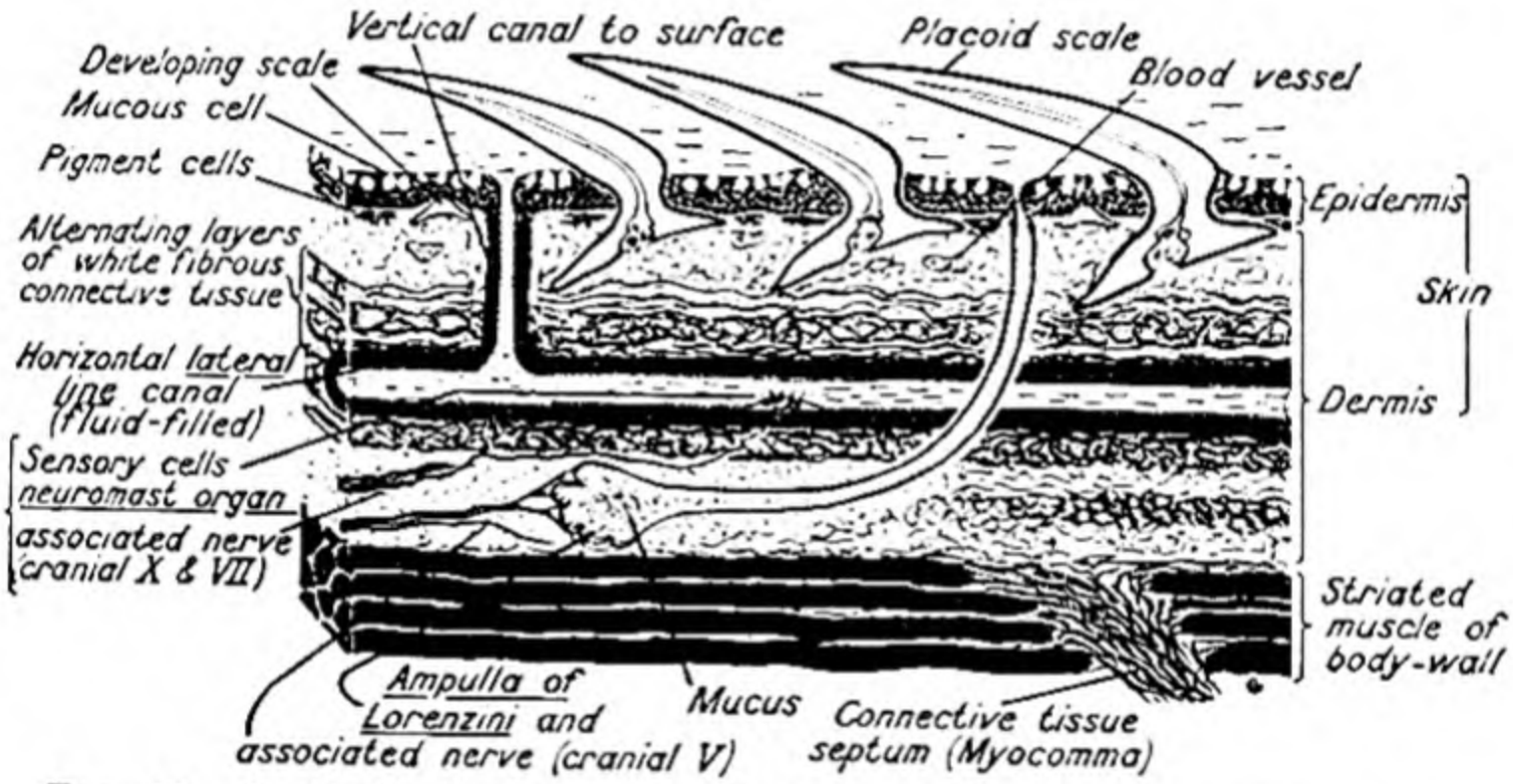


FIG. 57 – *Scyliorhinus*. Composite diagram of skin and sense organs.

epidermis itself may be further subdivided into a layer of actively-dividing cells at the base, known as the **stratum Malpighi**, and a more superficial layer of flattened, dead cells, comprising the **stratum corneum**.

The formation of scales is contributed to by both the epidermis and the dermis. A number of mesoderm cells in the dermis become collected together into a small group immediately beneath the epidemis 58, I). This latter becomes evaginated (Fig. 58, II), and the layer of epidermis lining the evagination forms the **enamel organ**. Meanwhile the mesoderm cells have become arranged in the form of a cone, projecting into the evagination, and they commence to produce dentine on the outer surface of the cone. This substance forms the main bulk of the scale, and over it the enamel organ secretes a cap of enamel. The base of the scale remains open, leading into the cavity of the scale, now known as the **pulp-cavity**. The base of the scale is of bony composition. Eventually the structure breaks through the surface of the skin as a fully-developed scale.

The spines on the ventral surface are single, whilst those on the dorsal surface are three-pointed. Those constituting the teeth possess a three-lobed base and a five-pointed crown. It should be observed that the spines on the claspers point in the reverse direction to those on the body, aiding the necessary grip during copulation.

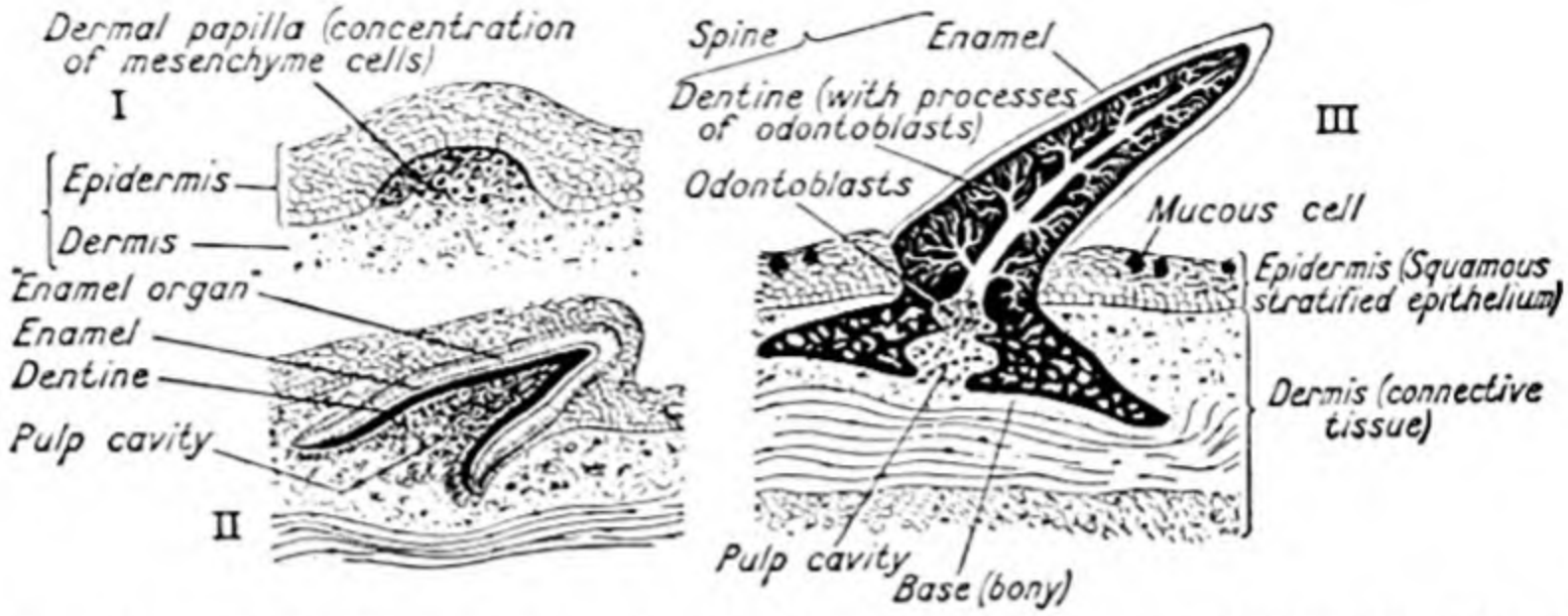
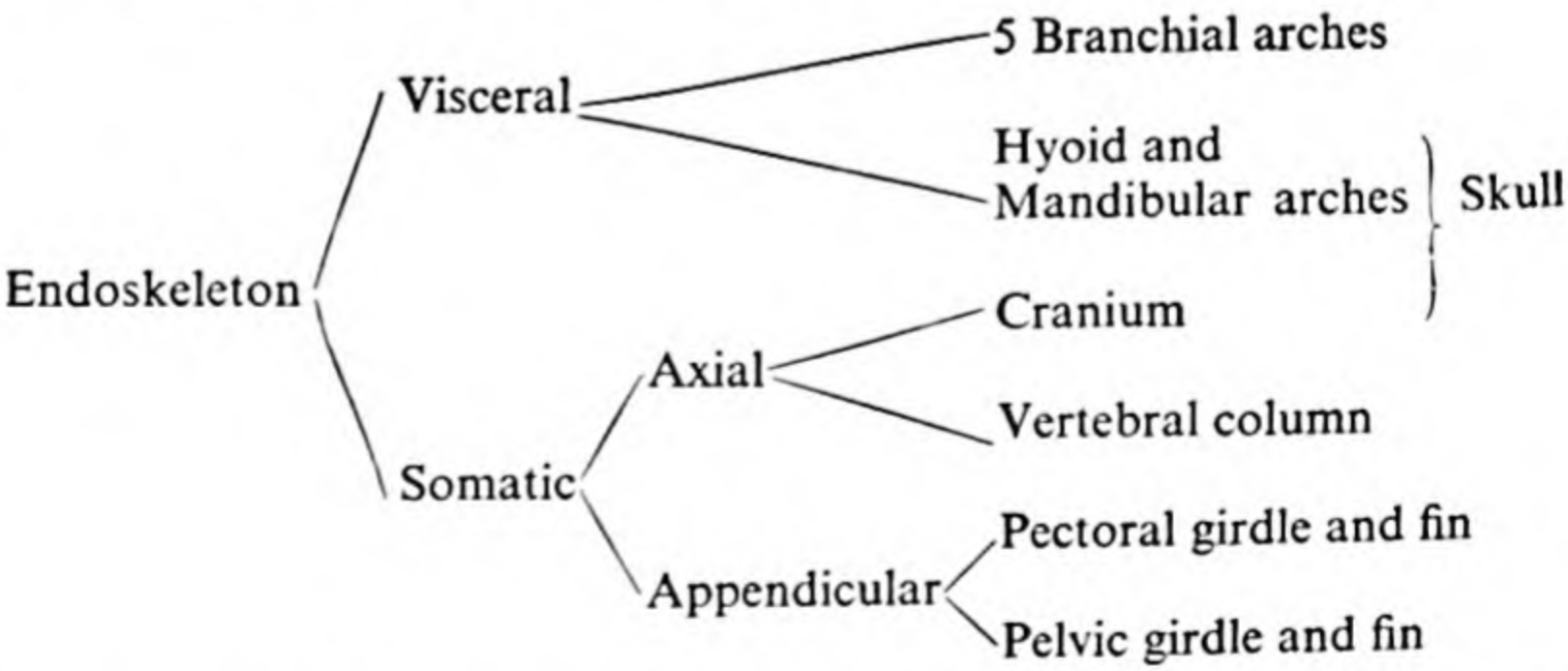


FIG. 58 – *Scyliorhinus*. Stages in the development of a placoid scale (dermal denticle).

As will be noted when the fins are being described, the webs of these organs are supported by horny **dermotrichia**, which are also skin derivatives.

Skeleton

The endoskeleton of the dogfish consists entirely of cartilage. It may be classified into component parts as follows:



It is essential to bear in mind throughout that the animal is segmented, and this is readily appreciated if the myotomes (muscle-blocks) are examined after removal of the skin. They do not lie straight across the body but are characteristically W-shaped. In the head the segmental arrangement of the muscles is obscured.

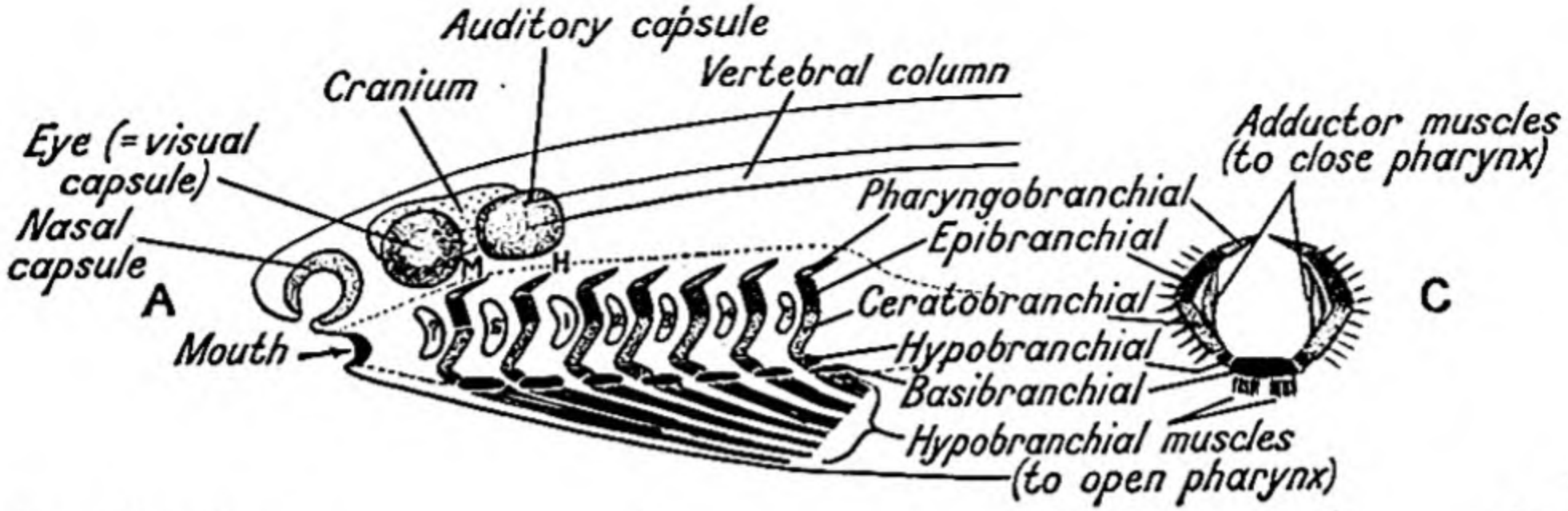


FIG. 59 – *A.*, Skull and visceral arches – ancestral condition (hypothetical). *B.*, *Scyliorhinus*. Skull and visceral arches (diagrammatic). *C.*, Transverse section of *A* in pharyngeal region. *D.*, Vertebral column – trunk region – side view. *E.*, The same – saggital section.

(A) VERTEBRAL COLUMN. The notochord is at first enclosed within a thick, fibrous sheath, covered in its turn by a thinner membrane. Soon sclerotomes (see page 518) give rise to a **skeletogenous layer**, investing the notochord and nerve-cord. The notochord is invaded by the cells of this layer, and thus a vertebral column, consisting of about 130 cartilaginous vertebrae, is formed.

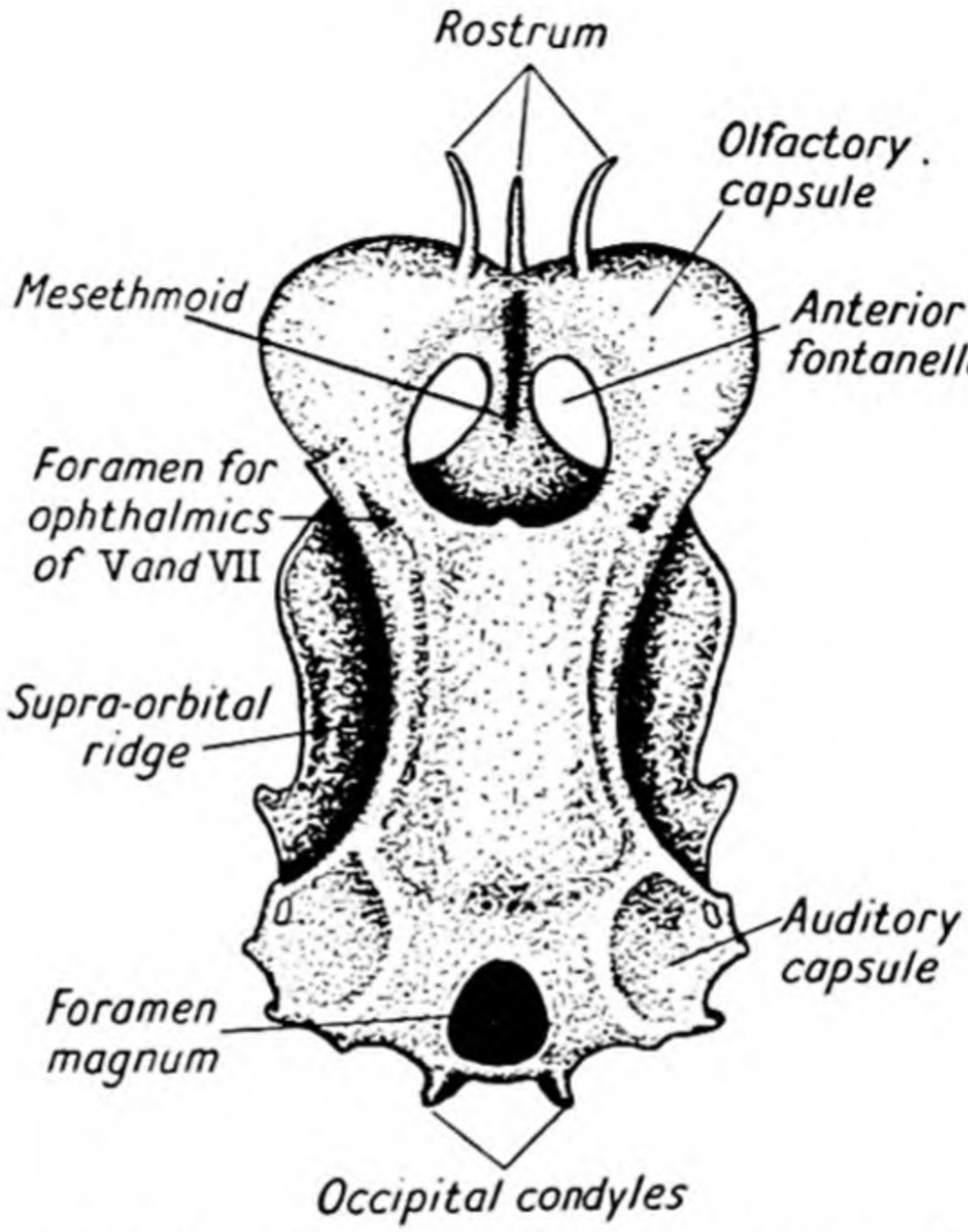


FIG. 60 – *Scyliorhinus*. Dorsal view of the neurocranium.

The centra are first formed, together with four pairs of cartilaginous plates per half body-segment: these plates arise as a result of the activities of cartilage-producing cells, termed **chondroblasts**. The posterior plates are the larger and are termed the **basi-dorsals** and **basi-ventrals**. The anterior pairs are the **interdorsals** and **inter-ventrals**. Reference to Fig. 59D will make it clear that both basi-dorsals and basi-ventrals contribute to the formation of the centrum of each vertebra, whilst the sides of the neural arches, which enclose the nerve-cord, are formed from the upper portions of the basi-dorsals and from the inter-dorsals. The roof of the neural arch is completed by two median concentrations of chondroblasts per segment, giving rise to the **supra-dorsals**. The notochord is invaded most deeply in line with the centre of the basi-dorsals and basi-ventrals, and the centra are finally concave at both ends, a condition known as

amphicoelous. The basi-ventrals become extended below the vertebral column to form the transverse processes and ribs, whilst the inter-ventrals disappear. In the tail region the transverse processes of opposite sides meet in the mid-ventral line to form the **haemal arch**, whilst ribs are absent. When development is completed there are two vertebrae per body-segment. This is regarded as an abnormal condition, confined to the caudal region of the vertebral column of *Scyliorhinus*.

(B) SKULL. This is essentially a hollow, cartilaginous case, known as the **cranium**, containing the brain. On to the front end is fused a pair of **nasal capsules**, whilst at the hind end occurs a pair of **auditory capsules**. The olfactory capsules themselves are open below, whilst their cavities are separated from each other by a **mesethmoid** cartilage. At the extreme anterior end is found a **rostrum**, formed by three processes projecting one from each nasal capsule and one from the mesethmoid cartilage. The cranium completely envelopes the brain in cartilage except for a membranous portion in the roof, known as the **anterior fontanelle**, situated at the line of fusion with the olfactory capsules. The pineal organ is attached to it. Placed laterally in the cranium is a pair of **orbits**, each protected by a surpra-orbital and sub-orbital ridge in the cartilage. Posteriorly the auditory capsules are continuous with the cranium and on their surface is indicated the position of the semi-circular canals of the ear, later to be described, whilst just on either side of the mid-line and between the capsules lies a small pore, communicating by a duct with the ear of its own side. The notochord has become completely replaced in the skull region, and an articulation is developed between the posterior region of the skull and the anterior end of the vertebral column. The brain being thus enclosed within the cranium, special apertures, known as **foramina**, must be pierced in the cartilage case to allow of the passage of nerves to and from the brain, as well as for facilitating a supply of blood to this organ. The disposition of these foramina is best studied practically. The structure so far described is known as the **neurocranium**, in contradistinction to the splanchnocranium, or **visceral skeleton**. The structure of this component of the skull of the dogfish is best understood by prior reference to the probable condition in the evolutionary ancestor. Here it is assumed to have consisted of seven jointed hoops of cartliage (better described possibly as pairs of half-hoops, since there is a median ventral element, but dorsally they remain separate). The first of these occurred behind the mouth, which was itself jawless, being suctorial. Subsequent pairs of these half-hoops occurred one behind each of the six pairs of gill-slits. The typical structure and nomenclature of a single component of this primitive visceral skeleton is shown diagrammatically in Fig. 61.

It is now easy to follow how the condition in the dogfish may have been derived. In the first arch, known as the *mandibular*, the pharyngo-, hypo- and basi-branchials disappeared, whilst the free ends of the epi-

and cerato-branchials turned forwards through 90°, elongated and converged at their forward extremities into the middle line, thus forming the jaws (*i.e.* **pterygo-quadrate** and **Meckel's** cartilages respectively). **A**

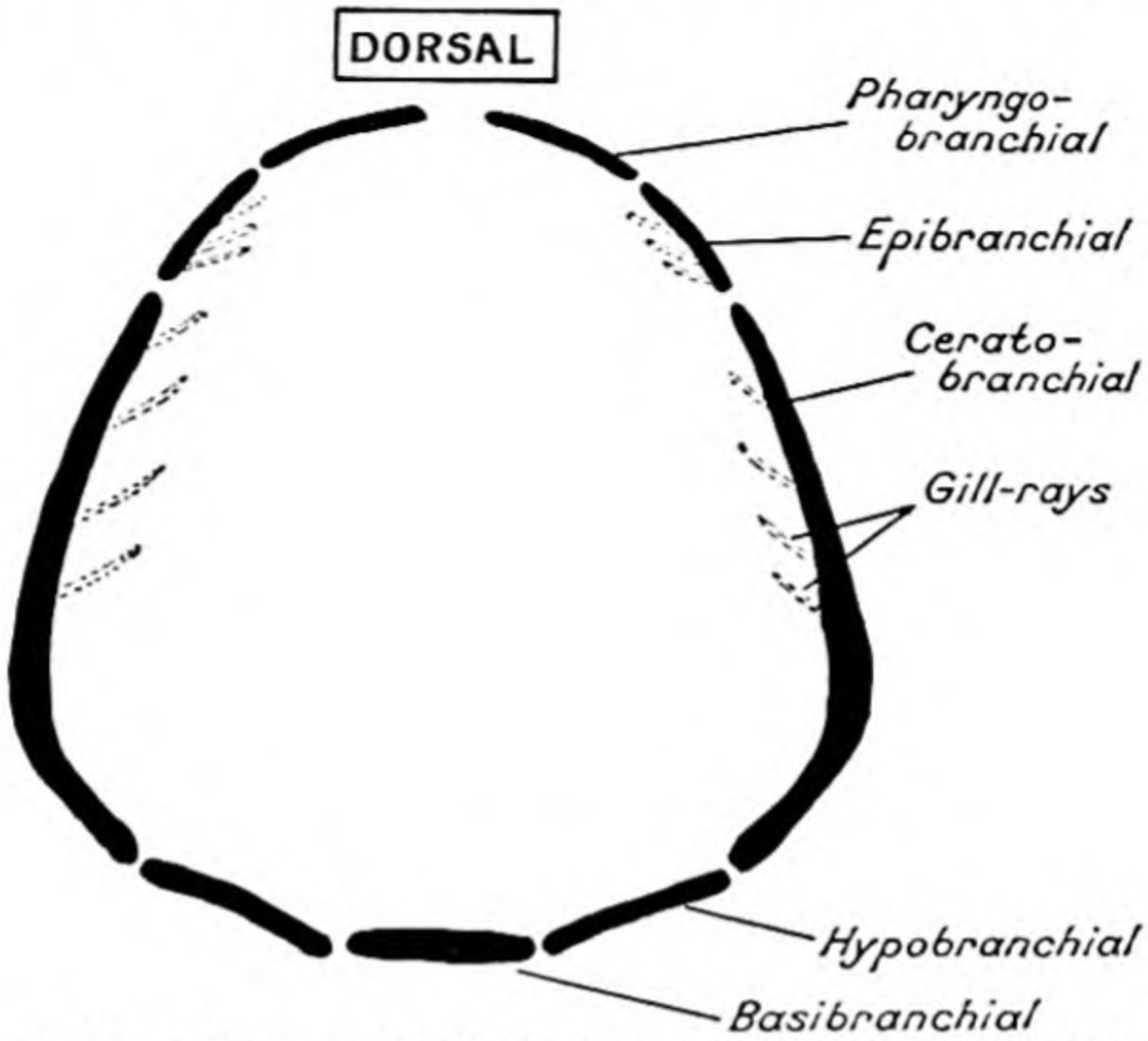


FIG. 61 – Diagram of typical visceral arch (primitive ancestral condition).

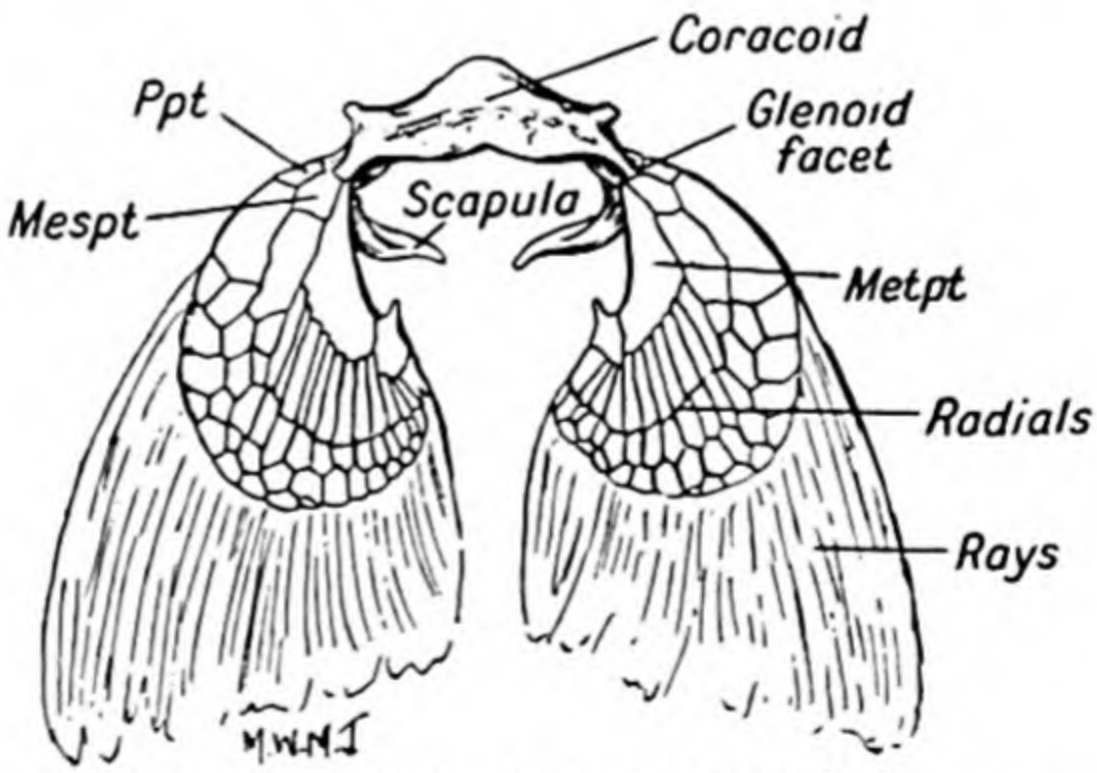


FIG. 62 – *Scyliorhinus*. Pectoral girdle.
Mespt., Mesopterygium; *metpt.*, Metapterygium; *ppt.*, Propterygium.

similar evolutionary fate overtook the second, or *hyoid*, arch, but here the surviving epi- and cerato-branchials became involved in the suspension of the jaws from the neurocranium, the epibranchial forming the **hyomandibula** and the ceratobranchial the **ceratohyal.** The basibranchial has persisted as the **basihyal.**

Attachment of the pterygo-quadrate cartilage to the neurocranium is completed by a **post-spiracular** ligament and an **ethmo-palatine** ligament. Such a method of jaw-suspension is termed **hyostylic.**

The remaining five arches, termed **branchial** arches, depart relatively slightly from the typical condition, the principal modifications being:

(*a*) The hypobranchial of the first branchial arch is attached to the basihyal.

(*b*) The hypobranchial of the fifth branchial arch is absent.

(*c*) The pharyngobranchials of the fourth and fifth branchial arches are united.

In this region there is also a median **basibranchial** plate. The pterygo-quadrate and the hyomandibula represent the epibranchials of their respective arches, whilst Meckel's cartilage and the ceratohyal correspond to the ceratobranchials of subsequent segments. The basihyal represents the basibranchial of the hyoid arch. The partitions between the gill-slits are strengthened by **extra-branchials** and **gill-rays.**

(C) FINS. The paired fins are anchored to the body by a pectoral and pelvic girdle and are supported by cartilaginous radials. The *pectoral girdle* is an almost complete hoop of cartilage, divisible into a median **coracoid** and a pair of **scapular** regions at the free, upward-directed extremities. On each side is a facet, known as the **glenoid surface,** separating the median coracoid from the scapular portion of the girdle and into which the fins are articulated. Each fin consists of three proximal cartilages, known (passing inwards) as the pro-, meso- and metapterygia. Articulating with these is a large number of jointed radials.

The *pelvic girdle* is a cartilaginous rod, lying transversely in the body-wall. At each end it articulates with a **basipterygium**, which itself bears a number of jointed radials along its anterior border.

The median fins are also supported by jointed cartilaginous radials, more numerous than the segments. The webs of all the fins are themselves supported by dermal **fin-rays,** or dermotrichia, very much more numerous than the radials which bear them.

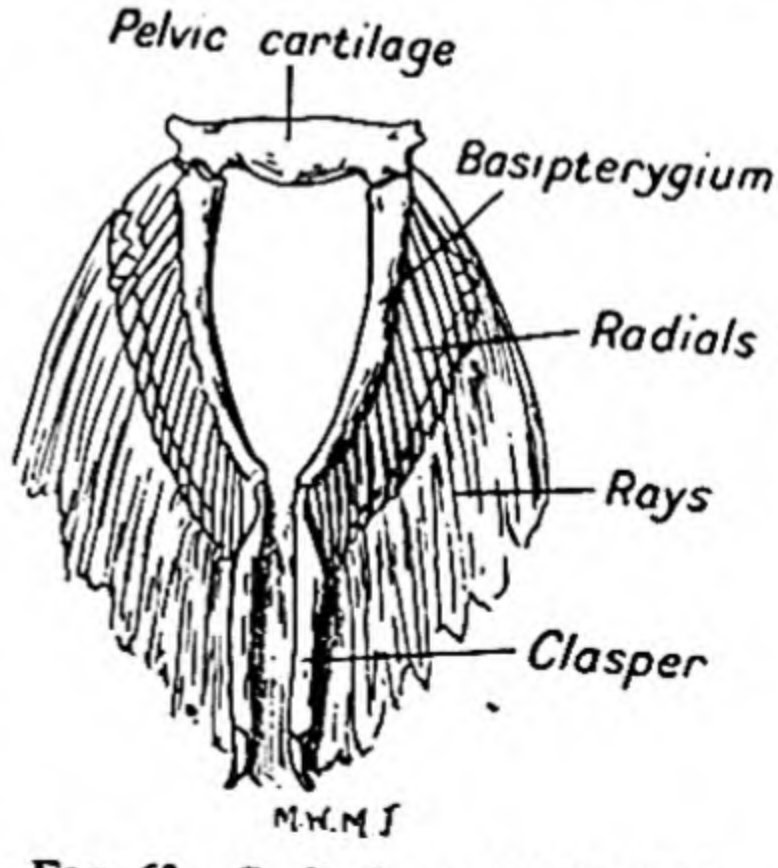


FIG. 63 – *Scyliorhinus*. Pelvic girlde.

Alimentary System

Around the margin of the jaws, as already noted, are the teeth. The lining of the buccal cavity contains many mucous glands, whilst from its floor there projects a non-protrusible pad of tissue, termed the *tongue* on analogy with higher

vertebrates, supported by the basihyal cartilage. This tongue assists in the swallowing of food. The buccal cavity leads into the **pharynx**, perforated laterally by five pairs of gill-slits and the spiracles, but the food is normally too large to be lost through them. The pharynx leads into an **oesophagus**, whose cavity is greatly restricted by deep folds in the lining. Thus only on swallowing will food and water be forced into the stomach, which lies beyond, the normal flow of respiratory water making its escape via the gill-slits. The stomach itself is U-shaped. The proximal (first) arm is known as the **cardiac** region, whilst the distal half is the **pyloric** region and is narrower. This is separated from the cavity of the intestine which follows by a **pyloric sphincter** muscle. A sphincter muscle is one surrounding an orifice and which, under normal conditions, is closed, only to be opened at intervals. Thus the muscle of the mammalian anus is a sphincter muscle. Immediately beyond the pyloric sphincter muscle is a very short, somewhat narrow region, known as the **duodenum**. Following this is the intestine, or **ileum**, a wide tube leading straight, but for one curve, to the cloaca. The internal surface-area of the ileum is increased by a fold in the endothelium, known as the **spiral valve**. At its posterior end the ileum narrows and loses its spiral valve to form the rectum. The liver is a large, bilobed structure attached to the coelomic wall by the **falciform ligament**. The gall-bladder is largely embedded in the under surface of the left lobe, and from it the bile-duct runs backwards to open into the duodenum. The **pancreas** lies in the bend between the stomach and the intestine. At its anterior end is a rounded lobe, from which a **pancreatic duct** enters the duodenum. The spleen, though not a digestive organ, is in close association with the stomach. It is a large, triangular organ, situated at the base of the U-shaped stomach, and with one arm projecting along the right side of the pyloric region. A small, dorsal diverticulum from the rectum constitutes the **rectal gland**. The process of digestion is described in detail in Chapter 23, and in principle it is similar in all the Chordata. It should be noted that no saliva is present in the fish. If present it would get washed out through the gill-slits with the respiratory current.

Respiratory System

As has already been mentioned the pharynx is perforated by five pairs of gill-slits (gill-pouches or gill-clefts) and a pair of spiracles, communicating between it and the exterior. These gill-slits slope backwards from their inner to their outer openings. The cavities of the gill-slits become enlarged within, and each wall (anterior and posterior) bears a number of richly-vascularised folds, or *lamellae*, forming the gills. Each lamella bears, at right angles to its main axis and on both sides, a large number of smaller lamellae, termed the *gill-filaments*. In this way a very large t al surface-area is created. The walls separating the gill-slits are sup- p rted by the skeleton of the visceral arches, the first true gill-slit (not

the spiracle) lying between the hyoid and the first branchial arch, whilst the spiracle occurs between the mandibular and hyoid arches. The last gill-slit and the spiracle each have a gill on their anterior wall only, that of the spiracle being termed a **pseudobranch**. The arches lying immediately in front of each gill-slit (including the spiracle) and behind

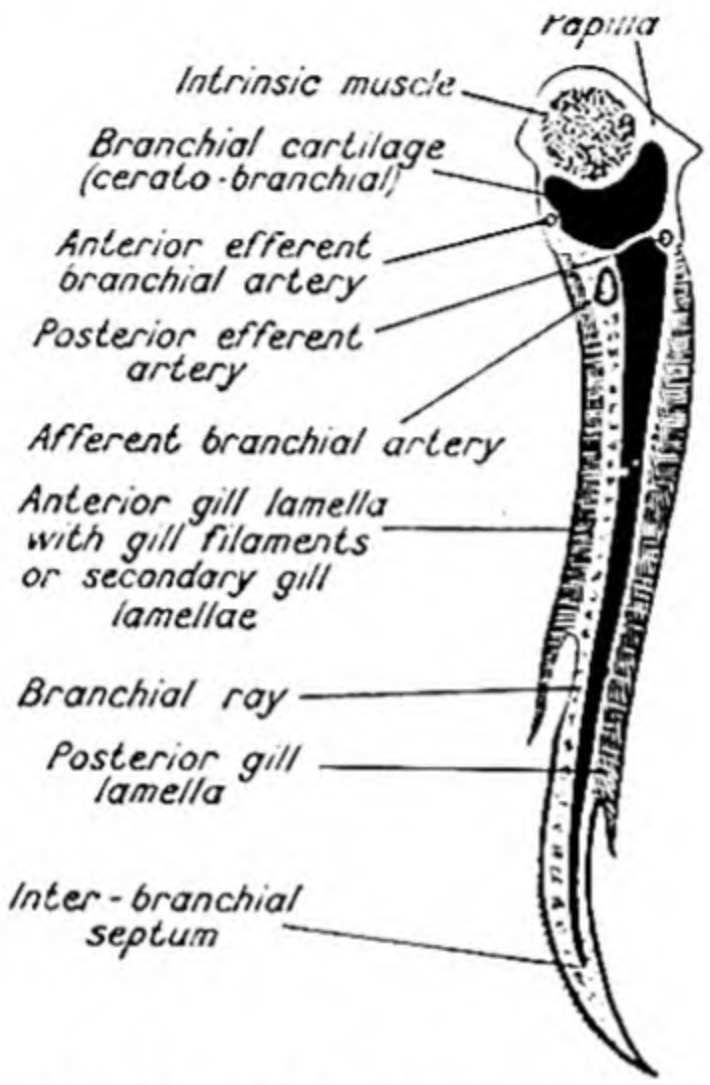


FIG. 64 – *Scyliorhinus*. Transverse section of a gill.

the last are known as the visceral arches, and are named the mandibular, hyoid and first to fifth branchial arches, as already indicated in the description of the visceral skeleton.

Ventiliation of the gills is effected by two distinct sets of movements, known respectively as inspiration and expiration.

Inspiration. This results in bringing water, carrying dissolved oxygen, to the gills. In this process the mouth is opened and the floor of the pharynx lowered by the contraction of the coraco-hyoid and caraco-branchial muscles, the oesophagus being closed meanwhile. Thus water is drawn into the buccal cavity and pharynx.

Expiration. This results in the expulsion of this water through the gill-slits. The movements are the reverse of those occurring at inspiration, and are caused by the contraction of the intrinsic muscles attached to the arches, and in particular to the epi- and cerato-elements, the coraco-hyoid and coraco-branchial muscles relaxing. The natural elasticity of the wall of the pharynx is also in part responsible. The oesophagus still remains closed.

Flaps of skin over the outer openings of the gill-slits prevent the entry

of water by that route at inspiration, whilst pulsating movements by the walls of the slits further assist the current, so much so that ventilation can be maintained even while the animal is feeding. In this connexion

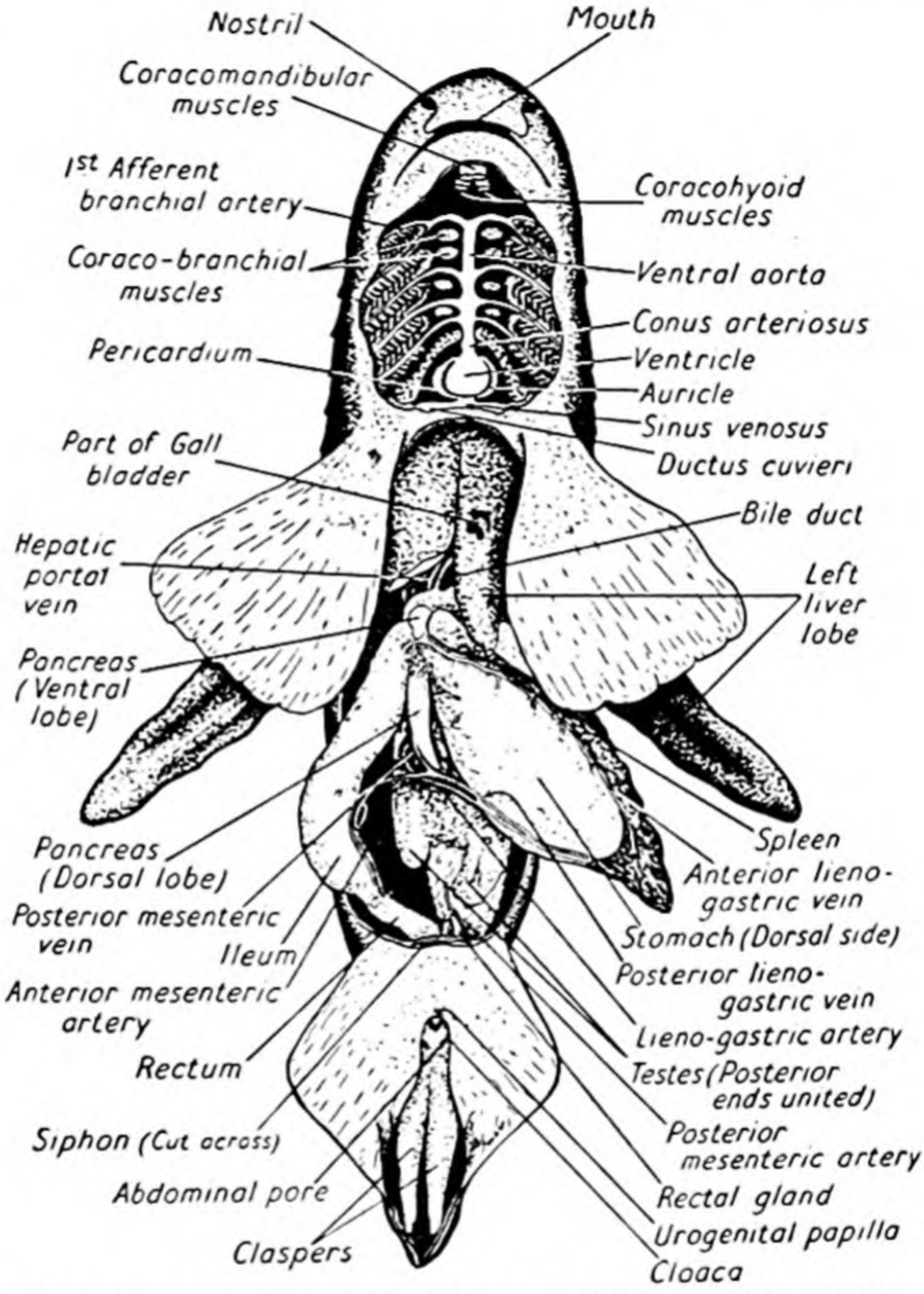


FIG. 65 – *Scyliorhinus*. Alimentary and afferent arterial systems.

it should be noticed that the spiracles can be employed as the means of entry of water.

As the water passes over the delicate gill-lamellae the dissolved oxygen is exchanged for carbon dioxide contained in the blood. The oxygen is absorbed by the haemoglobin of the blood for distribution to the tissues. Other exchanges also occur in this way. It is interesting to note that, while the embryo is in its capsule, long filaments protrude from

all six pairs of visceral clefs and probably play a part in the absorption of albumen. In the advanced embryo the pulsation of the throat mechanism can be seen, by which time there is probably a circulation of sea-water in the capsule.

Vascular System

This, as in all vertebrates, is of the *closed* type, corpuscles being retained within enclosing vessels (arteries, veins and capillaries) throughout the passage of blood around the body, though in many places there is an exchange of liquids and diffusion of solutes. The components of the system will be described separately.

The heart lies in the pericardial cavity, situated in the middle line between the posterior gill-slits. It is essentially an S-shaped structure. Posteriorly there is a thin-walled **sinus venosus**, into which is drained all the deoxygenated blood from the whole body. This chamber communicates anteriorly with a somewhat thicker-walled **auricle**, itself opening into a very thick-walled **ventricle**. From this passes forwards a narrow **conus arteriosus**, which penetrates the front wall of the pericardium to become the **ventral aorta**. Valves are situated at intervals in the heart to prevent the blood from 'sucking back'. The openings between the sinus venosus and auricle, and auricle and ventricle are thus guarded, whilst a double row of semi-lunar valves occurs in the conus.

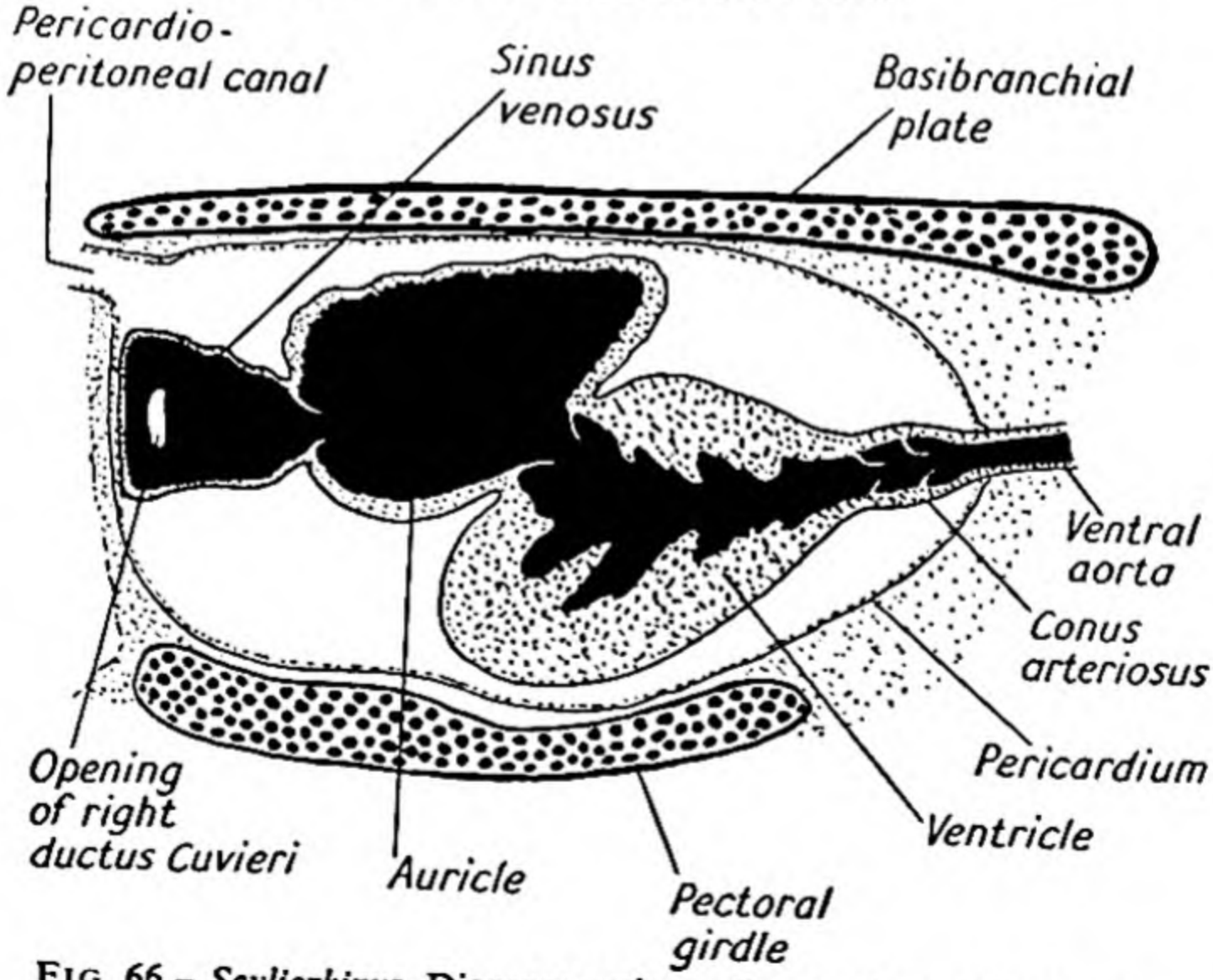


FIG. 66 – *Scyliorhinus*. Diagrammatic median section of the heart. Note that the auriculo-ventricular aperture is slightly to the right of the mid-line and would not strictly appear in such a section.

(A) ARTERIAL SYSTEM. Four pairs of **afferent branchial** arteries arise from the ventral aorta to supply blood to the gills. They run in the fourth, third, second and first branchial arches, whilst a branch originating in the hyoid arch passes forwards through the orbit to become the

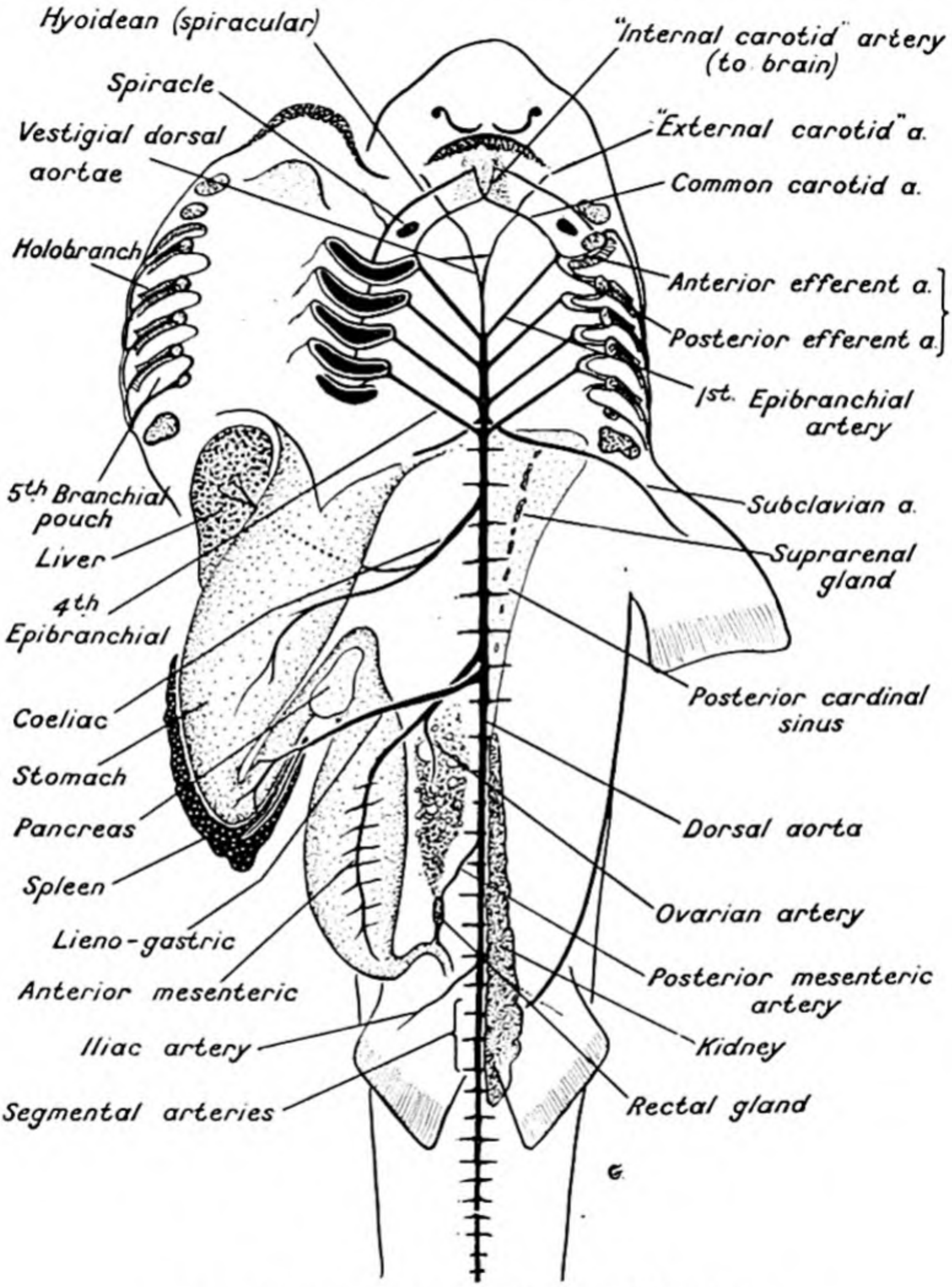


FIG. 67 – *Scyliorhinus*. Efferent arterial system.

main artery of the brain. After oxygenation at the gills the blood is collected up into four pairs of **efferent branchial** arteries. These form loops enclosing each of the first four pairs of gill-slits (not including the

spiracle). Since the last gill-slit has no gill on its posterior wall it has an efferent vessel along its anterior margin only, and from this blood is conveyed to the loop round the gill-slit next in front. From the dorsal end of each loop blood is conveyed away by an **epibranchial** artery in the roof of the pharynx, where these four pairs of arteries unite to form a **dorsal**

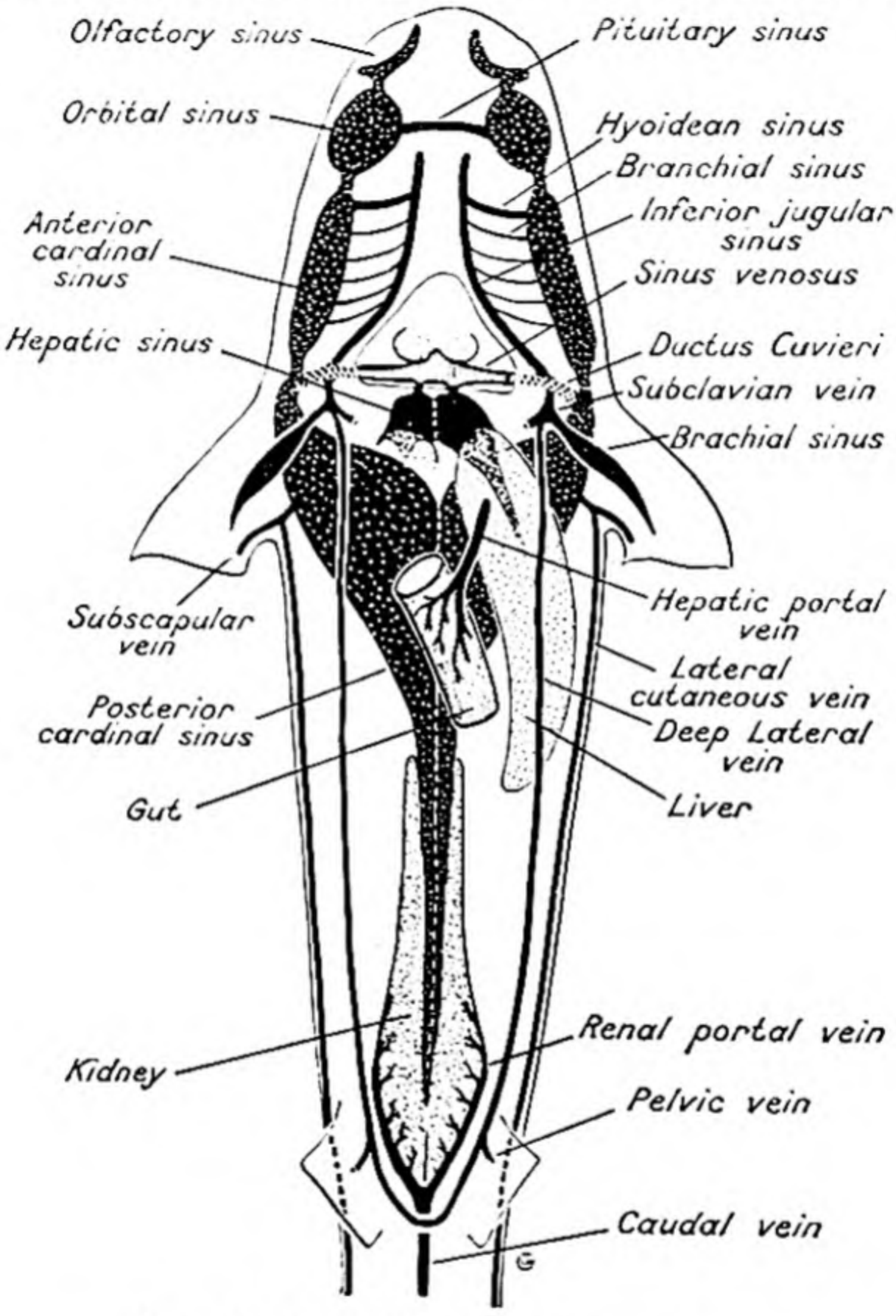


FIG. 68 – *Scyliorhinus*. Venous system.

aorta. Close to the origin of the first epibranchial artery there arises, on each side, from the corresponding efferent branchial artery, an artery which passes forwards, soon to be joined by an extension of the much reduced, forked dorsal aorta, forming the (*internal*) *carotid* artery. From this arises an *orbital* branch to vascularise the upper jaw and the snout. The two (internal) carotid arteries join but soon separate again to enter the cranium to supply the brain. The first efferent branchial artery also

bears anteriorly a *hyoid* artery, which supplies the pseudobranch of the spiracle before continuing forwards to join the (internal) carotid artery of its own side. Posteriorly the dorsal aorta extends throughout the whole length of the body, giving off a pair of **sub-clavian** arteries to the pectoral fins, just before it receives the last pair of epibranchial arteries. Further back it gives off a number of median vessels to the viscera, including (from in front backwards) a coeliac, an anterior mesenteric, a lieno-gastric, paired renals, a posterior mesenteric and paired iliacs, whilst it is continued into the tail in the form of a **caudal** artery. In addition to these major branches, segmented vessels also arise from the dorsal aorta to all trunk and tail segments.

(B) VENOUS SYSTEM. The veins of the dogfish are mostly peculiarly enlarged to form **sinuses**. Of these the principal ones are the anterior and posterior cardinal, and the hepatic sinuses. Blood from the liver is returned direct to the sinus venosus by a pair of spacious **hepatic** sinuses.

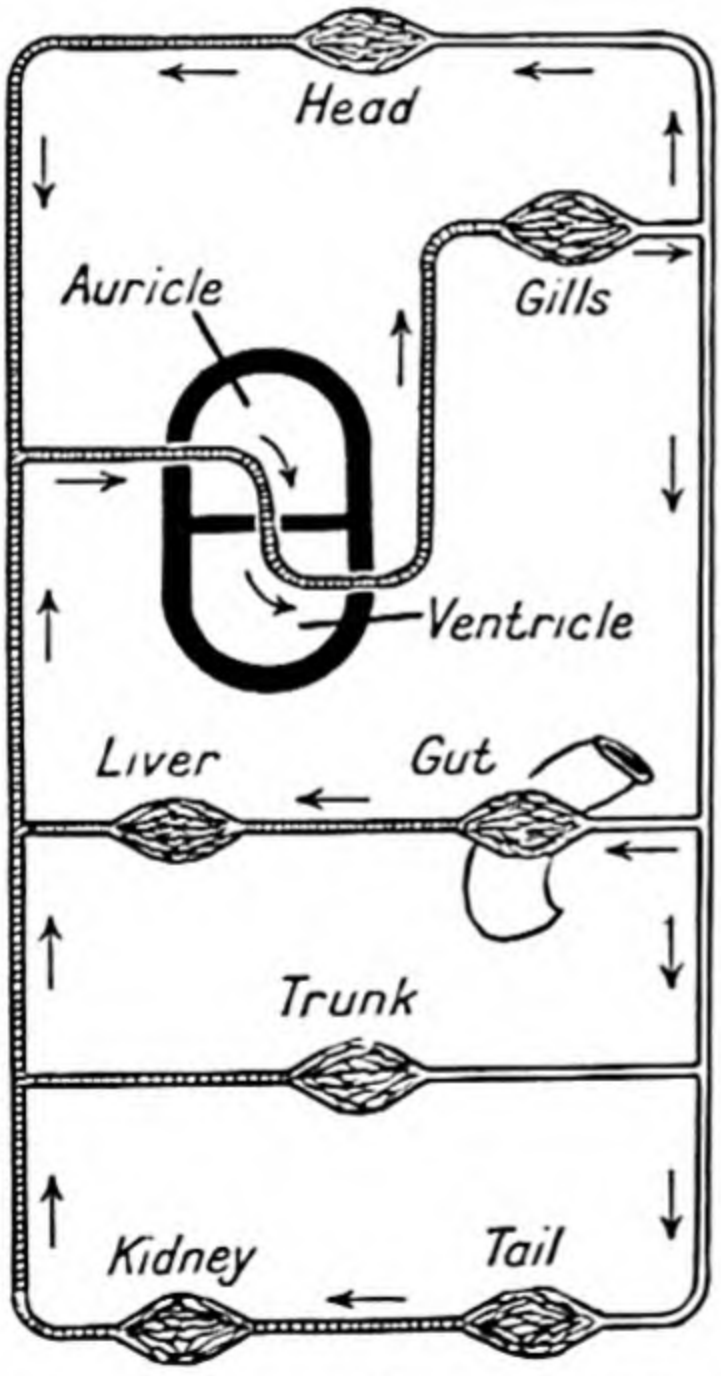


FIG. 69 – *Scyliorhinus*. Diagram to illustrate the course of circulation of the blood.

The anterior region of the body-wall is drained of blood by **anterior cardinal** sinuses and a pair of small **inferior jugular** sinuses. Each anterior cardinal sinus is continuous in front with an **orbital** sinus around the eye, and this, in its turn, is in connexion with a **nasal** sinus. The anterior cardinal sinus communicates with the inferior jugular sinus by a short **hyoidean** sinus, as well as with a vessel in each branchial arch. A **brachial** sinus from each pectoral fin is joined by the lateral vein of its own side to form the **subclavian** sinus, which opens into the ductus Cuvieri (see below). Each anterior cardinal sinus is continuous behind with a **posterior cardinal** sinus. This drains blood from the trunk, including the kidney of its own side. In the body-wall on each side runs a **lateral** sinus, returning blood eventually to the sinus venosus. All four sinuses – the anterior and posterior cardinals, the inferior jugular and the lateral of each side – unite outside the coelom, and blood is conveyed from each to the sinus venosus by a **ductus Cuvieri,** which runs across the coelom. Blood is returned from the gut to the liver by a **hepatic portal** vein. A **portal** vein is one which both originates

and terminates in the form of capillaries. Thus in the present case capillaries in the wall of gut become united to form the hepatic portal vein, which itself breaks up into capillaries again in the liver. There is also a **renal portal** system, for blood from the tail is collected up into a **caudal** vein which forks, one branch going to each kidney, in the tissues of which it breaks up again, before being carried forwards by a posterior cardinal sinus.

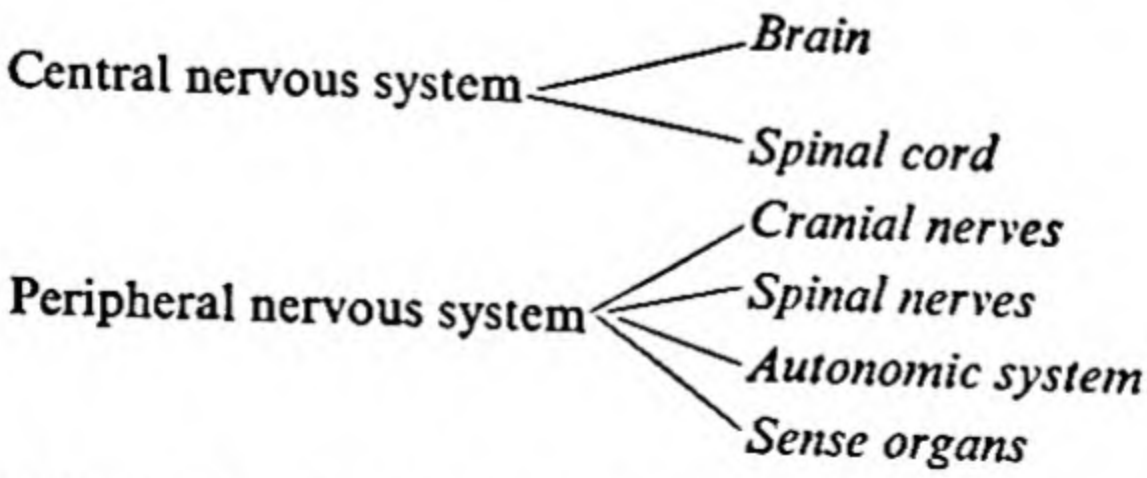
The heart of the dog-fish is described as **'venous'**. This is on account of the fact that only once in a journey round the body does the blood reach the heart. From here it is passed to the gills for oxygenation, and on leaving them it is distributed direct to various organs of the body without being first returned to the heart, as in higher forms. Thus the heart contains nothing but de-oxygenated blood, and it is therefore described as venous. After leaving the heart the blood must pass through at least two sets of capillaries – i.e. those of the gills and then of some other organ – before being returned. Should it get into the hepatic or renal portal vein it will have to pass through three sets of capillaries in all. Hence it is significant that blood is collected into large sinuses, thereby facilitating its flow.

Coelom

The coelomic cavity of the dogfish is divided into two regions by a septum; anteriorly there is a small **pericardium**, enclosing the heart, whilst the remainder of the viscera lie in the posterior **peritoneal cavity**. The two are in communication by a small pericardio-peritoneal canal, just below the oesophagus. To the anterior wall of the peritoneum is attached the liver by a falciform ligament, whilst a fold in the coelomic epithelium carries the hepatic artery and the hepatic portal vein; it is known as the **omentum**.

Nervous System

In order that the animal may function as a unit, and not as a number of separate parts, and so that it can respond to environmental conditions,



it is essential that a collection of organs be developed to perceive external (and in some cases internal) conditions, to convey messages (impulses)

about the body, and thus to effect integration. This is the function of the nervous system, the components of which may be classified as on page 97. Each of these components will be dealt with individually, although a more detailed consideration of the autonomic component will be left until later, when the subject of nervous integration is under review (page 466).

(A) BRAIN. The brain is clearly divisible into fore-brain, mid-brain and hind-brain, whilst the fore- and hind-brains themselves are further divided, each into two regions. Thus there are five parts in all to the brain, named from in front backwards the telencephalon, diencephalon (or thalamencephalon), mesencephalon, metencephalon, and myelencephalon. The structure of each region will be considered in turn. The most conspicuous feature of the telencephalon is a pair of large **olfactory lobes**, each associated with an olfactory organ (page 105). Behind, on the dorsal side, is the thickened cerebrum, showing an incipient tendency to paired nature.

The diencephalon is narrow and from its roof there projects a **pineal stalk**, terminating in a **pineal body**. Beneath the anterior part of its floor is found the **optic chiasma**, where the optic nerves intersect (see page 470). Posterior to this is the **pituitary body**, itself a composite structure, consisting of an *infundibulum* (from the floor of the diencephalon) and a

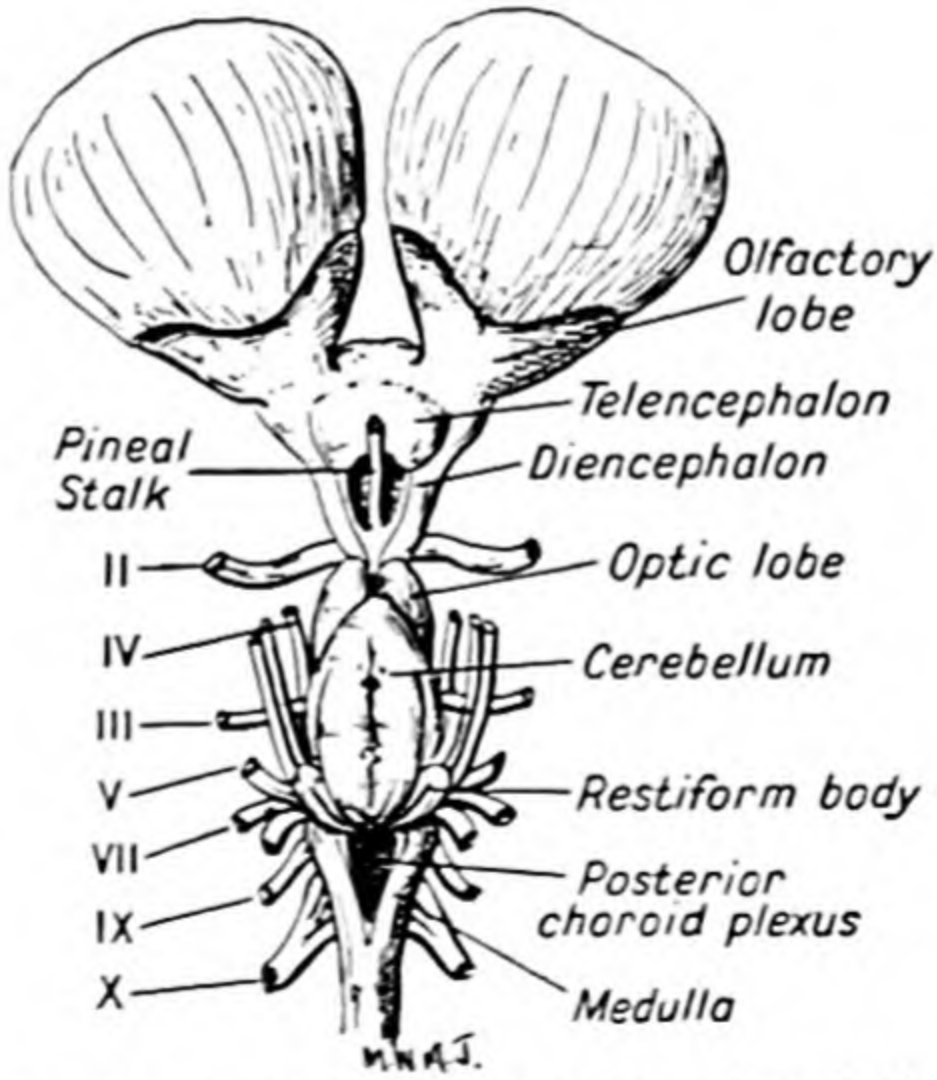


FIG. 70 – *Scyliorhinus*. Dorsal view of the brain.

hypophysis (from the roof of the buccal cavity). Laterally the infundibulum bears two *lobi inferiores*, whilst a pair of *sacci vasculosi* project from the floor of the diencephalon near the point of origin of the infundi-

bulum. The side walls of this part of the brain consist of thick tracts of nerve-fibres, forming the **thalami.**

The roof of the mesencephalon bears a pair of prominent **optic lobes,** whilst the floor is composed of thickened tracts – the **crura cerebri.**

The metencephalon is thickened dorsally to form the **cerebellum,** whilst behind it the myelencephalon remains thin roofed, forming the **medulla,** which passes insensibly into the spinal cord.

Like the spinal cord itself, the brain is tubular. The cavity of the fore-brain is known as the **third ventricle,** that of the hind brain the **fourth ventricle,** whilst that of the mid-brain between them is narrow and is

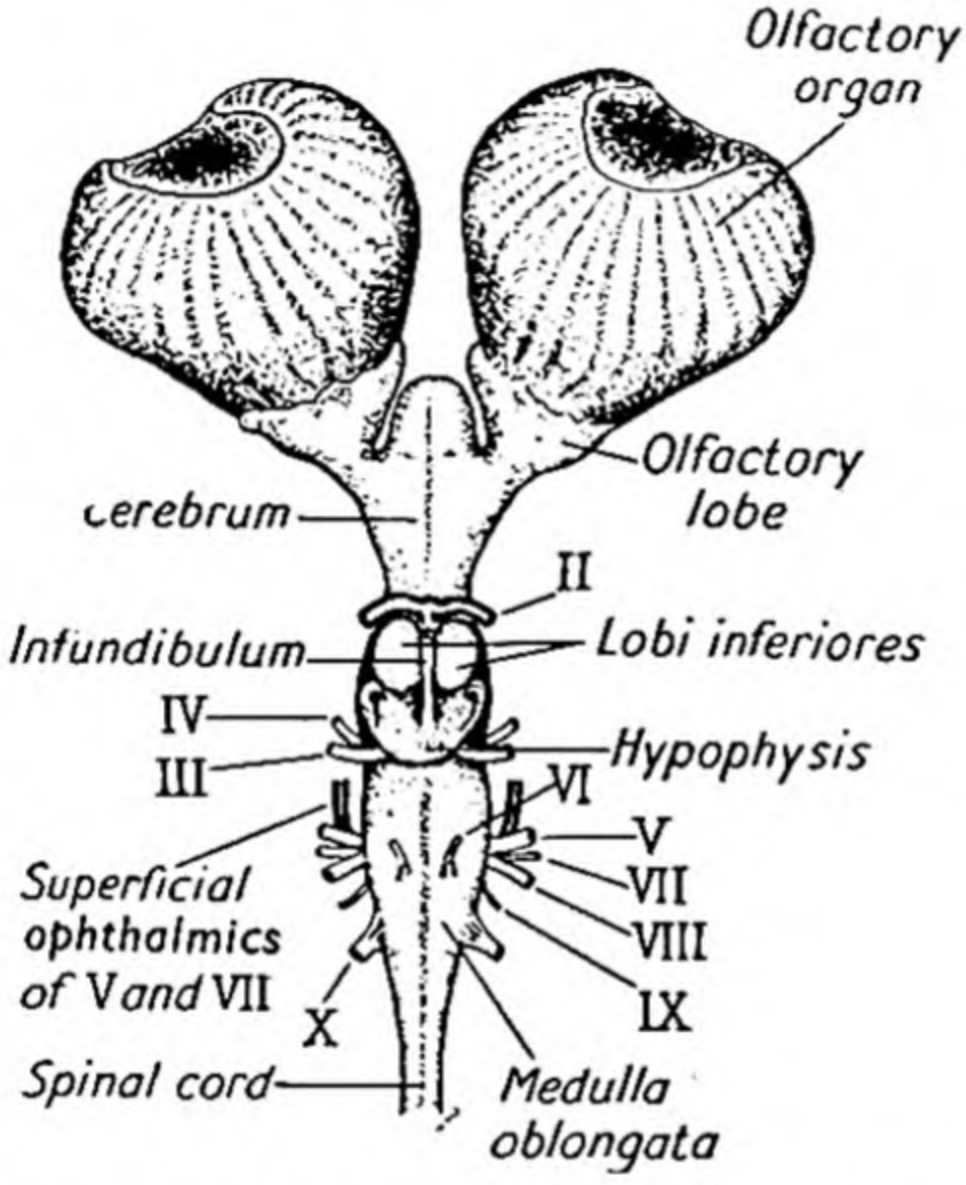


FIG. 71 – *Scyliorhinus*. Ventral view of the brain.

called the **aqueduct of Sylvius.** The whole brain is enclosed in a richly-vascularised membrane, known as the **pia mater,** which becomes much folded into the roofs of the third and fourth ventricles to form respectively an anterior and posterior **choroid plexus.** These plexus are important for the oxygenation of the cerebro-spinal fluid (page 131). Outside the pia mater occurs a harder and more protective membrane, known as the **dura mater.** In the brain the grey matter (nerve-cells) lies inside the white matter (nerve fibres) except in the cerebellum and optic lobes, where some of the nerve-cells are superficial. In the spinal cord the white matter almost completely encloses the grey matter.

(B) SPINAL CORD. The spinal cord arises from the hind end of the

medulla and passes dorsally along the whole length of the animal, being enclosed in the cavity of the vertebral column. It is covered by two membranous coats, similar to those of the brain, it is hollow and its cavity, continuous with that of the brain, is filled with cerebro-spinal fluid. Its structure is more fully described on page 461.

(C) CRANIAL NERVES. From the brain of the dogfish there arise ten pairs of cranial nerves, concerned principally with the innervation of the head, though the posterior ones are not confined to that region.

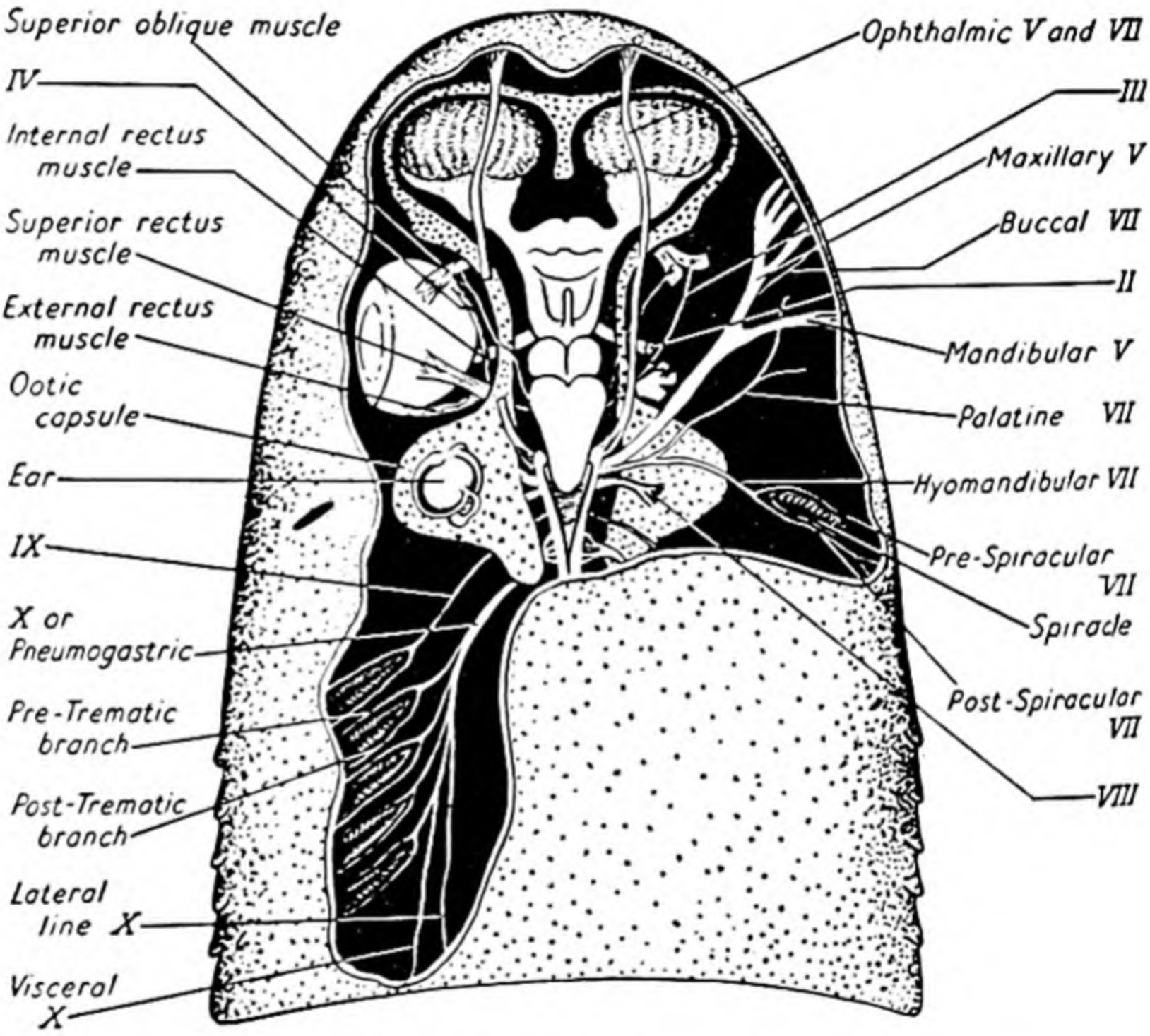


FIG. 72 – *Scyliorhinus*. Cranial nerves.
II–X., cranial nerves.

Their distribution is of great importance and they will be dealt with individually. The first nerve, referred to as No. 1 and called the **olfactory**, is not a true nerve at all. It is actually formed by the elongation of certain sensory cells of the nasal epithelium. These penetrate the fore-brain, but the cell-bodies remain in the epithelium. Similarly No. II, known as the **optic**, is formed merely as an extension, on either side, of the brain itself. It is important to notice that these nerves, emerging from the floor of

the diencephalon, cross before leaving the skull through the optic foramen on the opposite side to supply the eyeball. The region where this crossing occurs is known as the **optic chiasma**. At this point it is essential that the muscles by which the eye is rotated in the orbit be described, for nerves III, IV and VI are concerned with their innervation. Attached to each eye there are six muscles, connecting it with the wall of the orbit. Four of them are known as **rectus** muscles and they all arise close together near the hind margin of the orbit, subsequently diverging to become inserted at various points into the eyeball. The superior rectus and inferior rectus are inserted into the upper and lower sides of the eye respectively, whilst the internal rectus runs forward behind the eye to be attached anteriorly. The external rectus is the shortest of them all and is inserted into the posterior margin of the eyeball. Near the anterior end of the orbit arise two **oblique** muscles. The superior oblique runs on to the dorsal surface of the eye and its insertion occupies a position just anterior to that of the superior rectus. The inferior oblique muscle occupies a corresponding position in relation to the inferior rectus. Cranial nerve No. III is known as the **oculo-motor**, and supplies the superior, inferior and internal rectus and the inferior oblique eye-muscles. It arises from the ventral surface of the mesencephalon. No. IV is the **trochlear**, and is a slender nerve arising from the dorsal surface of the brain in the depression between the optic lobes and the cerebellum. It innervates the superior oblique muscle, whilst the external rectus is supplied by No. VI, a slender nerve arising from the ventral surface of the myelencephalon or medulla, and known as the **abducens**. Cranial nerve No. V is the **trigeminal**, so called on account of its division into three branches. It arises from the lateral surface of the myelencephalon and almost at once a superficial ophthalmic branch leaves the rest of the nerve to run forwards within the cranium, before emerging by a foramen to supply the skin of the snout region. The profundus branch, though disappearing in the dogfish, is represented in the closely allied skate, *Acanthias*. It runs forwards, through the orbit, beneath the superior oblique eye-muscle, to innervate the skin of the snout. The remaining two branches run together across the floor of the orbit to divide eventually into a maxillary branch to the upper jaw and a mandibular to the lower. Just after its emergence from the skull this nerve becomes enlarged to form the **Gasserian ganglion**. Cranial nerve No. VII, known as the **facial**, also arises from the ventral surface of the myelencephalon, and has a complicated distribution. A superficial ophthalmic branch runs forwards over the eye in company with the similar branch of the trigeminal and innervates the lateral line organs of the head. A buccal branch passes forwards beneath the eye to supply the lateral line organs of that region, having crossed the orbit within the main branch of the trigeminal. The palatine branch also crosses the floor of the orbit but posterior to the trigeminal, innervating the region of the upper lip. A

large hyomandibular branch runs across the hind wall of the orbit into the hyoid arch. The bulk of this nerve then passes posterior to the spiracle as a post-spiracular branch, but it gives off a small pre-spiracular in front of the spiracle. It supplies the lateral line organs of the lower jaw, described later. Cranial nerve No. VIII is the **auditory**, concerned in the innervation of the internal ear. It is to be regarded as a specialised branch of the facial nerve. No. IX is the **glossopharyngeal**, arising laterally from the myelencephalon. It supplies the lateral line of its region, and a pharyngeal branch passes to the gut. The bulk of the nerve runs behind the first gill-slit, giving off a small pre-trematic branch in front of it. The

Nerve	Name	Distribution
I	Olfactory	The nasal epithelium
II	Optic	The eye
III	Oculo-motor	All eye muscles except the superior oblique and the external rectus
IV	Trochlear	Superior oblique eye muscle
V	Trigeminal	
	(*a*) Superficial ophthalmic	Skin of the snout
	(*b*) Maxillary	The upper jaw
	(*c*) Mandibular	The lower jaw
VI	Abducens	External rectus eye muscle
VII	Facial	
	(*a*) Superficial ophthalmic	Lateral line above the orbit
	(*b*) Buccal	Lateral line below the orbit
	(*c*) Hyomandibular	Hyoid arch and lateral line of lower jaw
	(*d*) Palatine	Roof of the mouth
VIII	Auditory	The ear
XI	Glossopharyngeal	Pharynx and first branchial arch
X	Vagus	Second to fifth branchial arches Viscera and lateral line

vagus nerve, No. X, is the largest, and arises laterally by several roots just behind the glossopharyngeal. It emerges from the posterior end of the skull to run close to the anterior cardinal sinus of its own side. Soon after leaving the skull it gives off a branch to the lateral line, whilst it further supplies a pre- and post-trematic branch to each of the remaining four gill-slits. After giving off these branches it passes posteriorly to innervate the heart and stomach. The distribution of the cranial nerves

is summarised in tabular form on page 102, whilst on page 468 this is discussed in relation to the segmentation of the head.

(D) SPINAL NERVES. In every segment of the body behind the head, in the formation of which nine segments are incorporated (the term 'head' being taken here to include the whole branchial region, since this is innervated exclusively by cranial nerves, associated with the brain), there is a pair of fully-formed spinal nerves emerging from the spinal cord. Each consists essentially of two parts, namely a **dorsal root**, bearing a ganglion and entering the dorso-lateral corner of the spinal cord, and a **ventral root**, whose origin is ventro-lateral in position. On leaving the nerve-cord, these two roots become united almost at once, but soon separate again into a **ramus dorsalis**, supplying the sensory structures, a **ramus ventralis**, innervating the musculature of its own segment, and a **ramus communicans**, which connects each spinal nerve with a slender autonomic nerve-cord, running up on either side of the dorsal aorta. The structure and function of spinal nerves is more fully described on page 461.

(E) SENSE ORGANS. It is the collective function of the sense organs to acquire 'information' about an animal's environment, and they are accordingly differentiated for the specialised perception of different types of stimulus.

(i) *Neuromast System.* The neuromast system of the dogfish consists essentially of a tube, of ectodermal origin, but situated deep in the dermis. Its position is indicated superficially by the lateral line markings (page 83). Each tube opens at intervals to the surface, and consists, in parts, of sensory and supporting cells. The scattered groups of sensory cells lie on the floor of the tube and are connected by nerve-fibres with the main nerve-trunks beneath. The sensitive portions of the neuromast system respond to vibrations. On the head are scattered pits, known as **ampullae of Lorenzini**. These have been shown not to be part of the neuromast system, but to function as temperature receptors. The ear is a specialised member of the neuromast system, and its structure will now be considered.

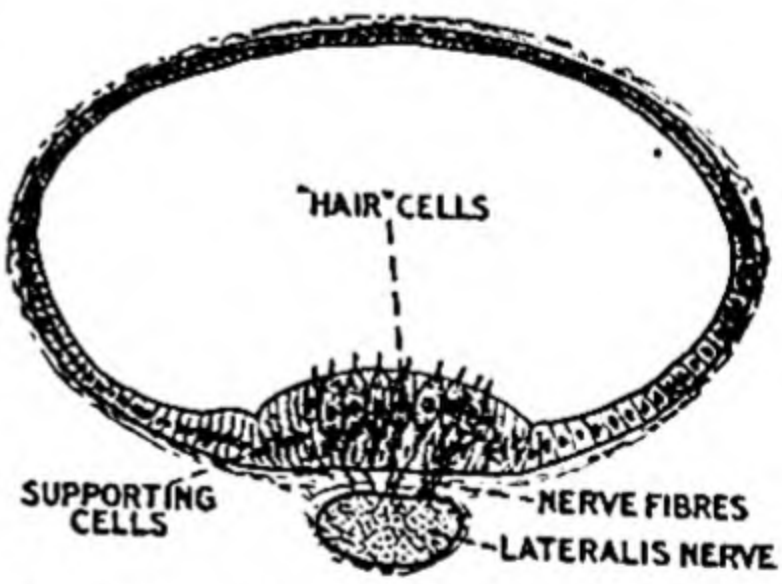


FIG. 73 – Diagrammatic transverse section of the lateral line of a cartilaginous fish. (From 'Animal Biology', by A. J. Grove and G. E. Newell. University Tutorial Press.)

(ii) *Ear.* This is essentially a pit which has become sunk in from the ectoderm. At its inner end it becomes constricted into a number of inter-communicating compartments, whilst it retains its connexion with the exterior by a

narrow tube – the **ductus endolymphaticus**. At the base this duct becomes enlarged to form two sacs – a dorsal **utriculus** and a ventral **sacculus** opening into it. Communicating with the utriculus are three **semi-circular canals**, known respectively as the anterior, posterior and horizontal, the first two lying vertical and at right angles to each other. Each canal ends in an **ampulla**, formed by a process of dilatation. The portion of the ear

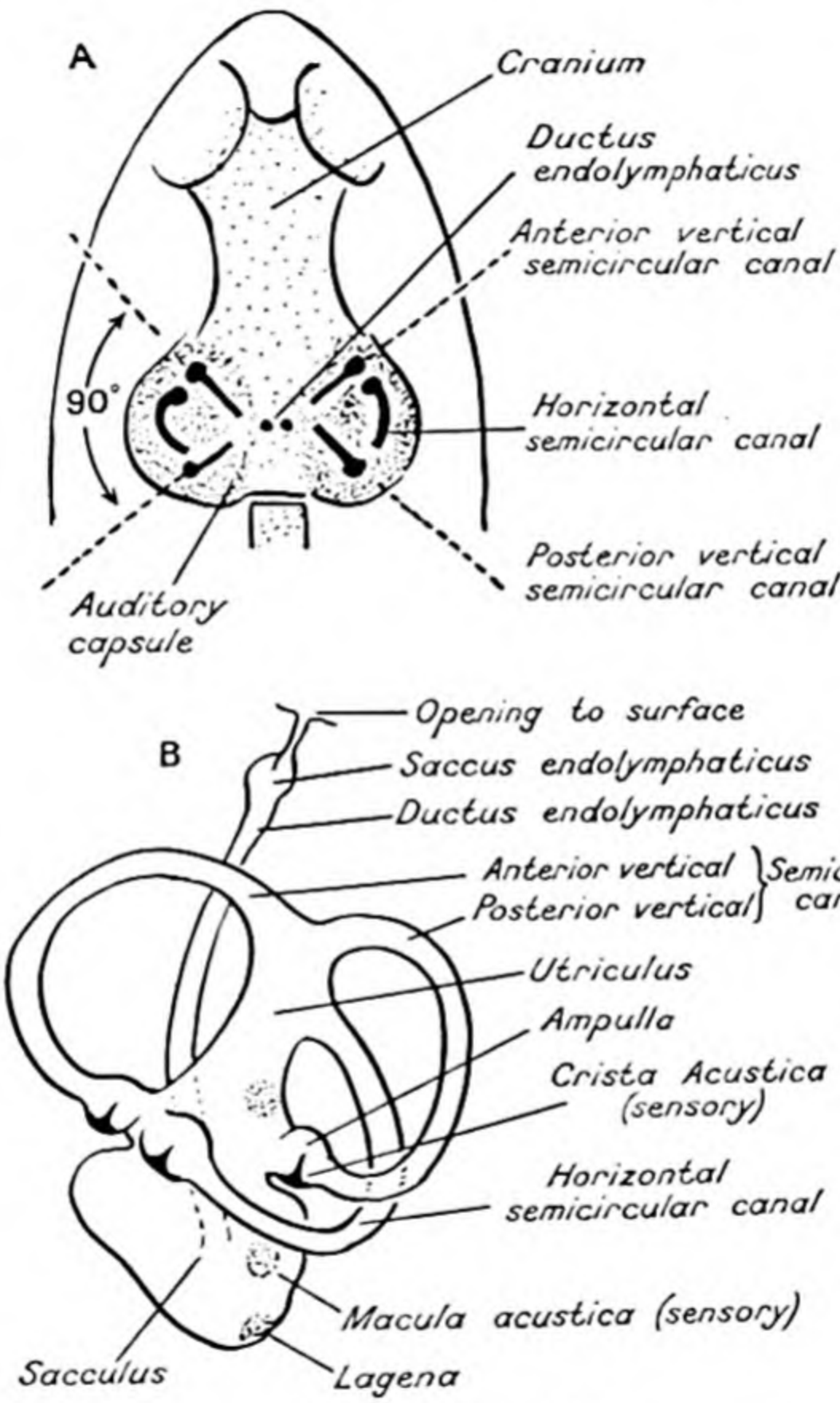


FIG. 74 – *Scyliorhinus*.
A., Diagram to show position of semicircular canals (dorsal view); *B*., Lateral view of internal ear.

so far described is termed the **membranous labyrinth**, and it is enclosed within a cavity of the auditory capsule, constituting the **cartilaginous labyrinth**. The membranous labyrinth contains a fluid, known as the **endolymph**, whilst it is supported in a further fluid, termed the **perilymph**,

being held in position by strands of connective tissue – the **trabeculae.** There are six patches of sensitive cells – one in each ampulla, one in the utriculus and two in the sacculus. Those in the ampullae are termed **cristae** and the remainder **maculae.** These resemble essentially the sensitive portions of the neuromast tubes, and they are stimulated as a result of change in orientation by the movements of calcareous bodies, known as **otoliths,** contained in the endolymph. The cristae detect movements in space, whilst the maculae perceive the pull of gravity. It is interesting to notice that in most fish a diverticulum of the sacculus – the **lagena** – contains a further patch of sensitive cells, whilst in the carps and their allies a thin region in the wall of the auditory capsule is connected with the air-bladder by a chain of small bones, termed the *Weberian ossicles.*

(iii) *Eyes.* A comparison with those of a mammal, fully described in Chapter 8, will be found on page 170.

(iv) *Olfactory Organs.* These are particularly well developed in the dogfish, for they afford its principal guiding influence when in search of food. There is a pair of olfactory organs situated in the anterior end of the head. Each is a sac-like organ, enclosed in an olfactory capsule. Its lining is thrown into a number of primary and secondary folds, thereby increasing the surface, and the endothelium is highly sensitive. Each organ opens to the exterior by a nostril, but, unlike higher forms, the nasal chamber is not in communication with the buccal cavity.

Urino-genital System

This system is responsible for the elimination of liquid waste matter, as well as for the production and liberation of germ-cells, but since to some extent the same organs are employed the system is treated as one composite whole. It is essential at this stage to indicate the general course of vertebrate kidney development. In the higher vertebrates (reptiles, birds and mammals) this occurs in three phases, consecutive kidneys being termed the **pro-, meso-** and **meta-nephros.** In fish and Amphibia only the first two phases are represented. This topic is discussed more fully on page 612. In the dogfish the pronephros develops as a series of tubules, opening at one end by ciliated funnels, or **nephrotomes,** into the coelom, and at the other into a longitudinal **pronephric duct,** leading to the cloaca. The pronephros quickly disappears, however, to be replaced by a second set of tubules, opening into the duct already established, which is now termed the **Wolffian duct.** In both sexes this duct opens into the cloaca on a median papilla, whilst this newly-formed mesonephros constitutes the functional excretory organ of the adult. In the male the most anterior tubules become connected with the seminiferous tubules (page 347) of the testis, forming the **vasa efferentia.** Thus the Wolffian ducts serve for the elimination of both urine and seminal fluid, whilst only the posterior portion of the mesonephros is excretory. But in the female the original pronephric duct becomes longitudinally constricted

to form both a Wolffian duct and a **Müllerian duct** (or **oviduct**), the latter retaining its anterior connexion with the coelom and functioning for the evacuation of eggs. There is no urinary bladder in *Scyliorhinus*.

(A) MALE. There is a pair of large testes, attached to the dorsal wall of the coelom. Spermatozoa, bound up in groups of about fifty, forming

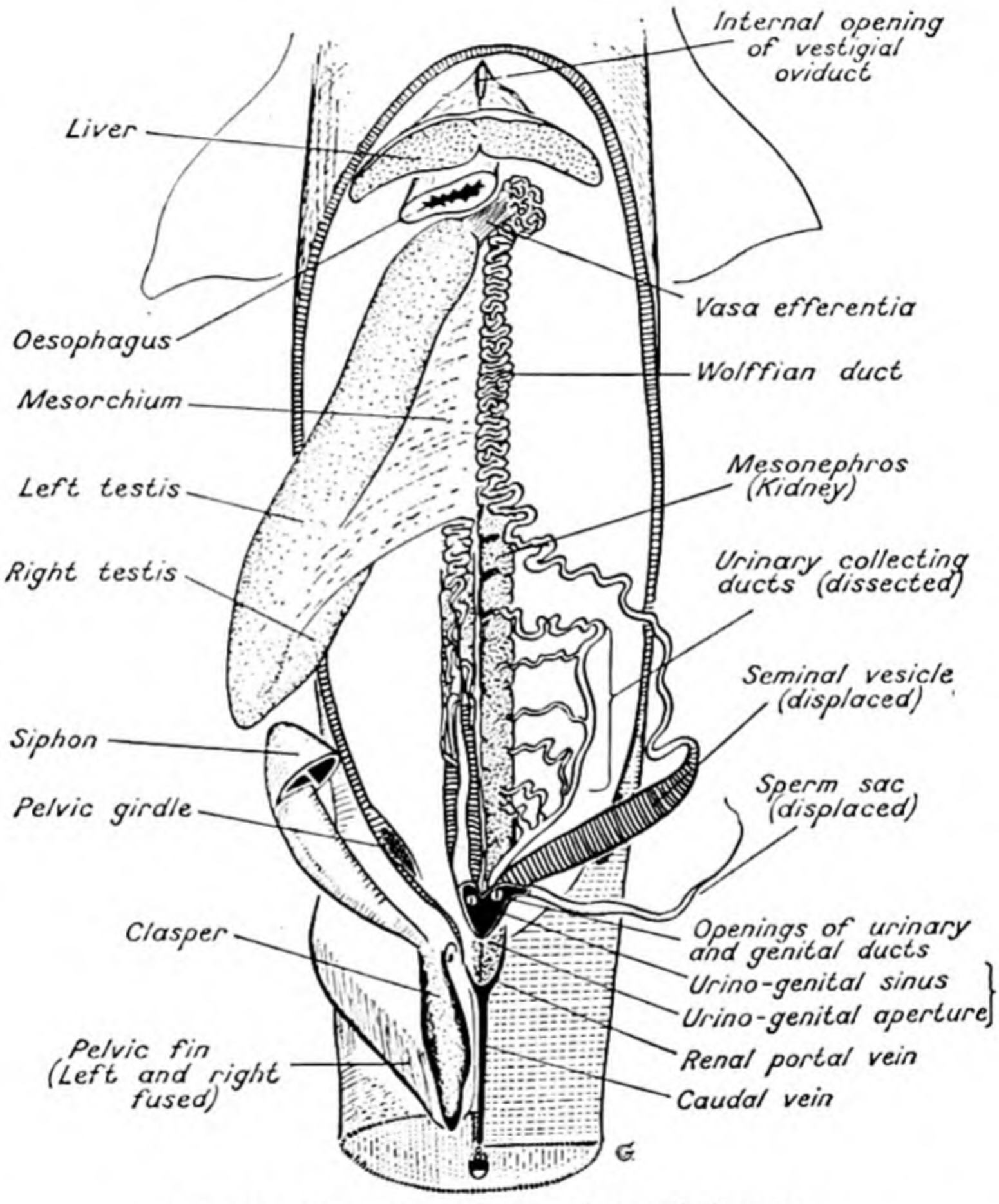


FIG. 75 – *Scyliorhinus*. Male urino-genital system.

spermatophores, are conveyed away from each to the anterior end of the corresponding mesonephros by a number of fine tubules, known as the **vasa efferentia**, which are the original kidney tubules of that region. Thus the sperms are carried to the **Wolffian duct**, which itself becomes very much coiled, and is frequently known as the vas deferens. This becomes

swollen at its posterior end to form a vesicula seminalis, where sperms are stored. The excretory products from the posterior portion of the mesonephros are passed into a collecting duct, which unites with the Wolffian duct at the base of the seminal vesicle. These conjoined tubes then open into a sperm-sac, and the sperm-sacs of the two sides become united to form a **urino-genital sinus**, itself opening into the cloaca on a urino-genital **papilla**.

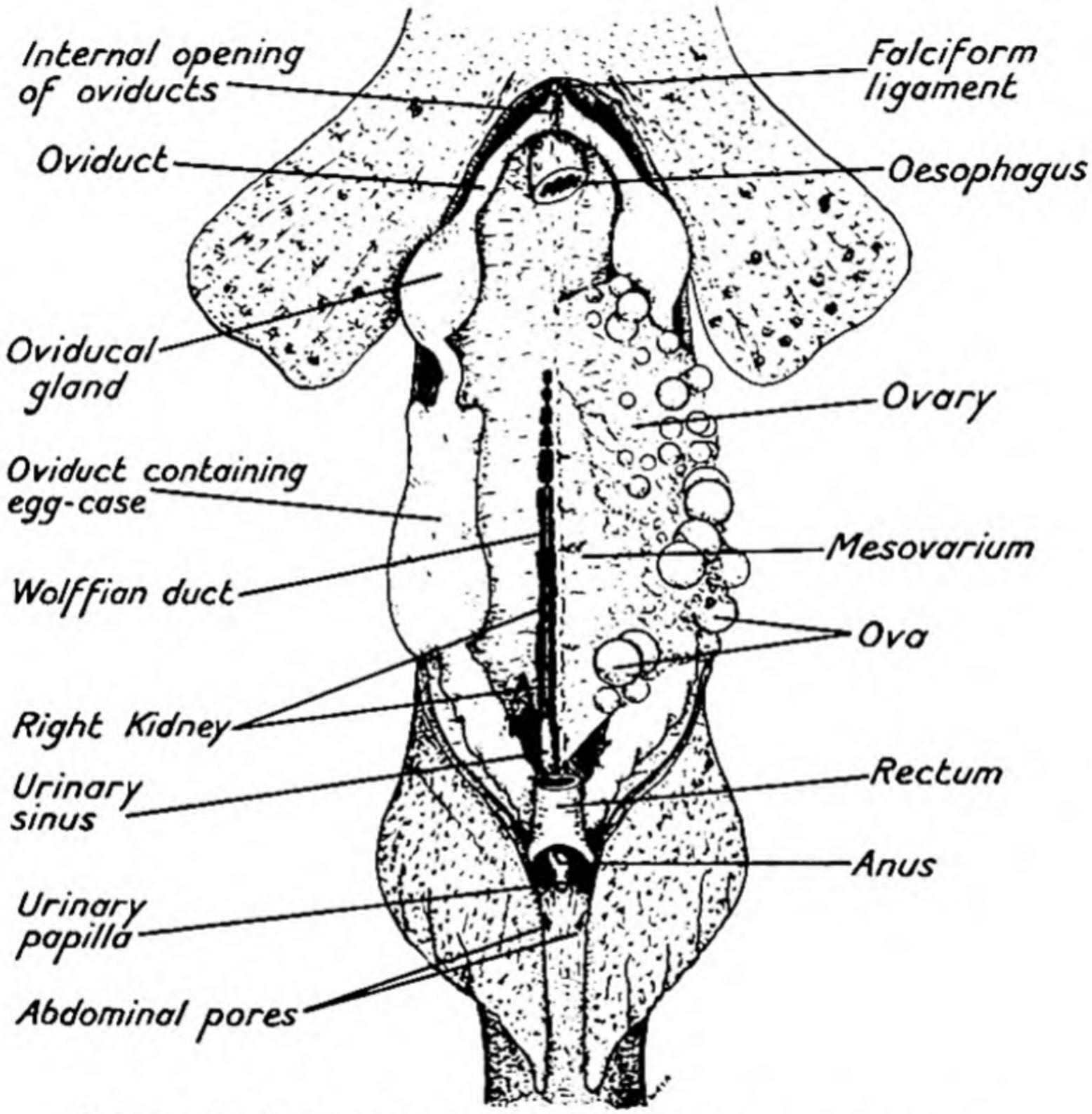


FIG. 76 – *Scyliorhinus*. Female urino-genital system. The ovary has been displaced to the left side.

(B) FEMALE. There is present an ovary on the right side only, attached to the dorsal wall of the coelom by a mesentery, termed the **mesovarium**. Eggs, when ripe, are shed into the coelomic cavity, from which their only escape are provided by the **Müllerian ducts**. These open funnel-wise at the **ostium** on the ventral side of the oesophagus and pass uninterrupted to the cloaca. The passage of eggs into the ostium, a journey requiring

several hours, is largely effected by ciliary action (page 330). The distribution of cilia is very precise in the mature female, where their activity is continuous in both pregnant and non-pregnant states. The principal areas of ciliation are – (i) the wall of the peritoneum generally; (ii) the walls of the oviducts and the inner side of their supporting mesenteries; (iii) the mesovarium; (iv) parts of the liver lobes, bile-duct, hepatic portal vein and hepatic sinuses, and (v) the falciform ligament. The cilia are most numerous and most active in the immediate vicinity of the ostium. The ostium is itself the opening of the *right* oviduct, into which the left one opens just above the ostium. Some short distance behind the ostium a swelling on each oviduct marks the position of the **oviducal gland**. This is divisible into three regions. The first is concerned with the secretion of albumen, the second of mucus and the third of egg-case material. The endothelium (page 329) of each zone is composed partly of ciliated cells and partly of tubular secretory cells, whilst the lumen of the gland is considerably restricted by projecting lamellae. In the shell-secreting zone spermatozoa may be stored for long periods in the crevices between the lamellae.

Thus the mesonephros is here purely excretory in function and does not aid in the evacuation of genital products. The associated Wolffian ducts each become swollen posteriorly to form a urinary sinus, opening by a median **urinary papilla** into the cloaca. The Müllerian ducts are represented in the male merely by a pair of vestigial funnels on the ventral side of the oesophagus and by the sperm sacs.

Semen is transferred from male to female by the aid of the claspers of the former. Fertilisation occurs in the shell-secreting zone of the oviducal gland, albumen having been previously added to the eggs and the egg-cases about three-quarters formed. As soon as the latter are completed they are liberated by passage down the remainder of the oviduct. Each is drawn out at the four corners into filamentous processes, by means of which attachment to seaweed is effected. The whole in this condition is known as a 'Mermaid's purse', and early development, occupying several months, takes place within the case.

It appears probable that copulation occurs in deeper waters and spawning near the coast. Investigation suggests that breeding continues throughout the year except for the months August to October, with each female laying about ten eggs per month.

Endocrine Organs

The significance of these organs is considered in Chapter 27. It is sufficient here briefly to indicate their structure and disposition.

An ectodermal invagination from the roof of the mouth becomes intimately connected with a downgrowth from the floor of the brain. These two processes are known as the **hypophysis** and **infundibulum** respectively, and together they constitute the **pituitary body**.

A depression in the floor of the mouth becomes completely closed off from the buccal cavity to form the **thyroid gland**, visible in dissection as a pear-shaped organ situated between two large bands of muscle.

A **thymus** gland on each side is constituted by a number of glandular masses in the roofs of the gill-slits, lying in close association with the anterior cardinal sinus.

Between the posterior ends of the kidneys, arising from the coelomic epithelium, is a structure known as the **inter-renal body**, whilst lying at intervals along each autonomic nerve-cord is a mass of tissue, of nervous origin, termed the **supra-renal body**.

Others present include the islets of Langerhans (embedded in the pancreas), the pineal body (above the roof of the hind end of the fore-brain) and the gonads.

PRACTICAL WORK

As well as the usual examination of external characters, followed by dissection of the alimentary, urino-genital, venous, afferent arterial, efferent arterial and nervous systems, in that order, the skeleton should be studied and drawn. This can be prepared by keeping the animal in 70% alcohol for some days, and then immersing it for a few minutes in almost boiling water. The soft parts can then be removed, and the skeleton thus obtained is best kept in diluted alcohol (20%).

Boil a little skin in potash solution, so that the scales may be readily removed. Mount dry or straight into Canada balsam.

CHAPTER 7

Rana Temporaria

The common frog, *Rana temporaria*, is found in damp grass-land in Britain, usually in the vicinity of streams or ponds. In winter it undergoes a sort of hibernation in holes and crevices near ponds, where it remains quiescent until the following spring.

External Features

The body of the frog is clearly divisible into head, trunks and limbs. There is no neck present, the head passing insensibly into the trunk. Locomotion is effected mainly by the hind limbs, which have become specially strengthened in adaptation to the frog's hopping mode of progression. The skin varies in colour from olive-green through varying shades of brown to orange, and the colour can be changed slowly. On the head may be seen a pair of bulging eyes, the upper lids of which are thick, opaque and almost immovable, whilst the lower lids, which can be drawn upwards across the eye, are thin and transparent. It is important to notice that this latter lid does not correspond to the lower eye-lid of mammals, this being entirely absent in the frog. It is a third-eye-lid, represented in mammals by the nicitating membrane, situated in the inner corner of each eye. Just in front of each eye is a small nostril, whilst posterior to each eye is an ear-drum, or tympanum. There is no external ear, or pinna, and in higher forms it will be observed that the tympanum itself has become sunk in beneath the surface of the head, thus affording protection. The fore- and hind-limbs are similar in structure, though the hinder ones are considerably larger and have five well-developed toes, whilst the front ones have only four. Each is typically divisible into three regions – the upper limb, the fore-limb and the hand or foot. The hand and foot are similarly divisible. There is a proximal wrist (carpus), a palm (metacarpus) and fingers in the hand, and corresponding ankle (tarsus), instep (metatarsus) and toes in the foot. The male frog, during the breeding season, may be distinguished from the female externally by the presence on the first finger of the former of a roughened thumb-pad which assists in the process of copulation. Situated slightly dorsal to the posterior extremity of the trunk is a small, rounded aperture, known as the cloaca. Through this faeces (solid waste matter), urine, and eggs or sperm are shed. Such a common aperture is termed a cloaca, in contradistinction to the anus of higher forms, through which only solid waste

matter is voided. Thus in this respect male and female frogs show no external distinction.

Skin

The skin of the frog is always moist, owing to the production of mucus by glands occurring at intervals over the entire surface. This mucus is important for two reasons. The frog breathes a great deal through its general body-surface when on land, and exclusively by this means when submerged for long periods. Thus when on land it is essential that the skin be kept moist so as to facilitate a rapid gaseous exchange. This phenomenon was encountered in the earthworm. Furthermore, this mucus, on account of its unpleasant taste and slimy nature, may afford the frog some protection from its enemies. Contained in the skin is a large number of pigment spots, each composed of a collection of pigment cells. According to environmental conditions these cells may become expanded or contracted, and the animal thus becomes darker or

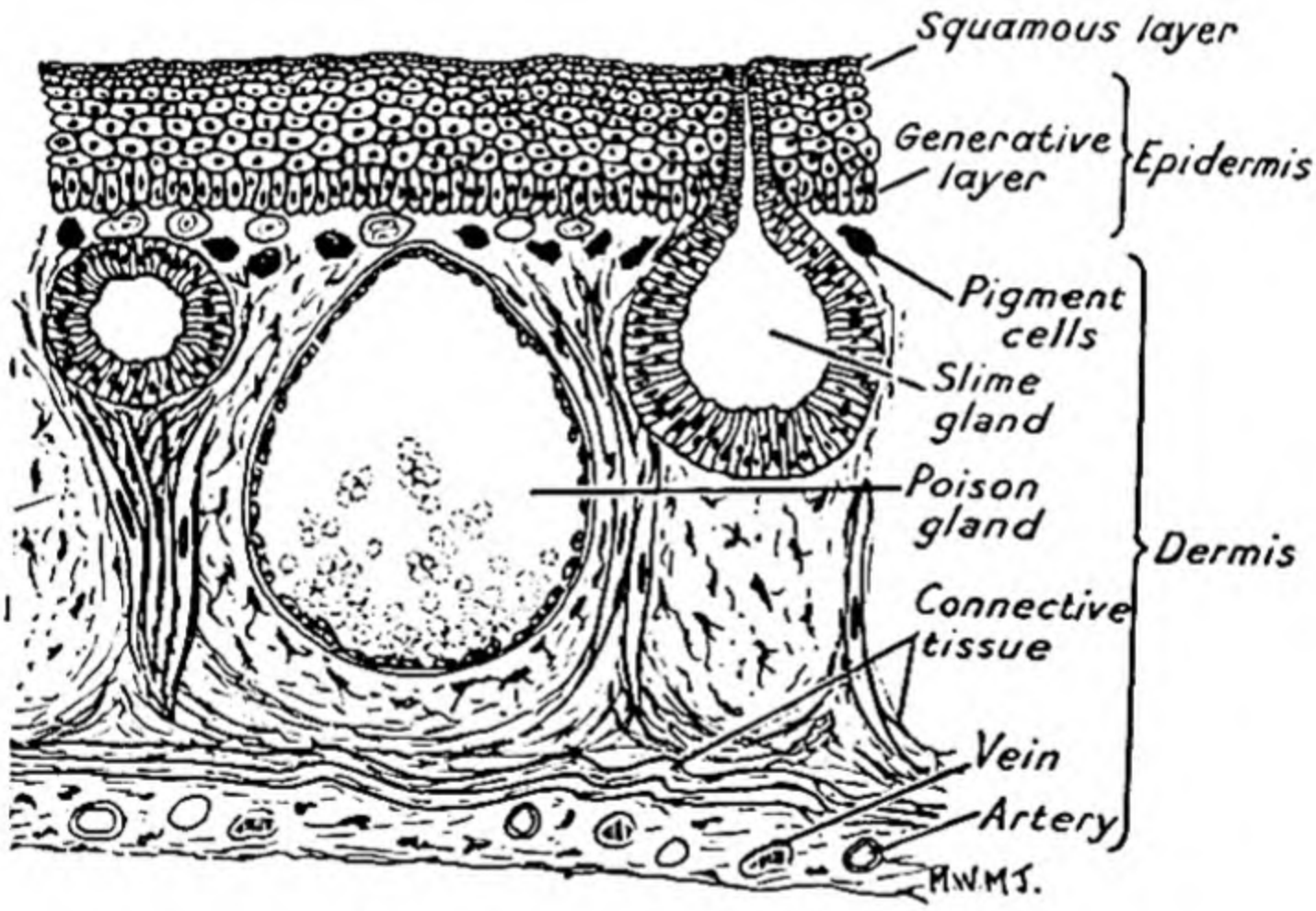


FIG. 77 – *Rana*. Vertical section of the skin.

lighter in colour. Wet, dark or cold conditions cause expansion of the pigment cells. In this way some sort of protection may be effected by a simulation of the shade of the environment. The outermost layer of the skin is horny and is shed at intervals and devoured by the frog. The skin lies loose over the body-wall beneath, from which it is separated by a number of subcutaneous lymph-sacs (page 129). It is held in position by underlying connective tissue (page 322).

The detailed structure of the skin can be made out only by examination

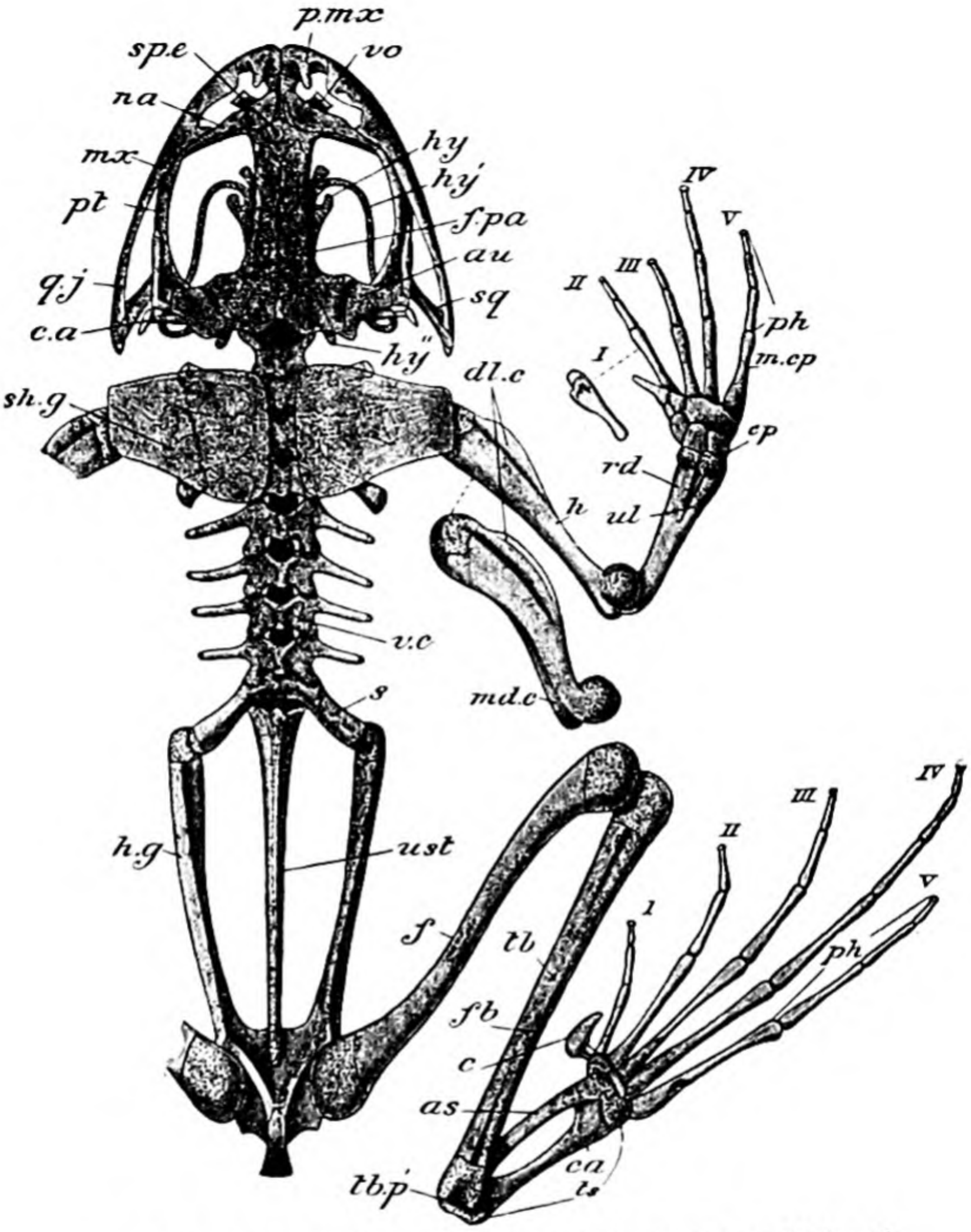


FIG. 78 – *Rana*. Skeleton, from the dorsal side. (From 'Atlas of Practical Elementary Zootomy', by G. B. Howes. Macmillan.) *as.*, astragalus; *au.*, auditory capsule; *c.*, calcar; *c.a.*, columella auris; *ca.*, calcaneum; *cp.*, carpus; *dl.c.*, deltoid crest; *f.*, femur; *fb.*, fibula; *f.pa.*, fronto-parietal; *h.*, humerus; *h.g.*, pelvic girdle; *hy.*, hyoid, body; *hy.*, hyoid, anterior cornu; *hy".*, hyoid, posterior cornu; *m.cp.*, metacarpals (metatarsals not specially lettered); *md.c.*, medial crest; *mx.*, maxilla; *na.*, nasal; *ph.*, phalanges; *p.mx.*, premaxilla; *pt.*, pterygoid; *q.j.*, quadratojugal; *rd.*, radius; *s.*, sacrum; *sh.g.*, pectoral girdle; *sp.e.*, sphenethmoid; *sq.*, squamosal; *tb.*, tibia; *tb.p'.*, tibio-tarsal joint; *ts.*, tarsus; *ul.*, ulna; *ust.*, urostyle; *v.c.*, vertebral column; *vo.*, vomer; *I–V.*, digits.

of a prepared section under a microscope. It presents an appearance as in Fig. 77. It is primarily divisible into two layers, namely a superficial epidermis, bordered on its inner side by the dermis. The epidermis itself may be further subdivided into an inner **stratum Malpighi**, or Malpighian layer, situated next to the dermis and consisting of actively-dividing cells, and a **stratum corneum**. The products of division of the stratum Malpighi pass towards the surface and become flattened and lifeless to constitute the stratum corneum. The dermis consists mainly of smooth muscle and connective tissue (page 322), containing blood-vessels and mucous glands, the latter being invaginations of the epidermis. The pigment layer lies close to the surface of the dermis.

Skeleton

The skeleton consists mainly of bone, but a certain amount of cartilage is present. It is divisible into an **axial** skeleton, made up of skull and vertebral column (backbone), and an **appendicular** skeleton, composed of limbs and limb-girdles.

(A) SKULL. The skull is divisible into a number of more or less distinct regions. Thus the brain is enclosed in a case, known as the **neurocranium**, to the anterior end of which is fused a pair of nasal capsules and to the posterior end a pair of auditory capsules. The sclerotic coat (page 166) of each eye represents a capsule, composed of fibro-cartilage and not fused on to the cranium. Below the neurocranium occurs the visceral skeleton, highly developed in the dogfish, but in the frog represented only by the skeleton of the jaws, by the hyoid apparatus in the floor of the mouth, and by the columella of the ear. The whole is so arranged as to enclose a pair of large orbits, into which the eyes fit. They differ from the orbits of higher forms in that the eyeballs of the frog are not separated from the cavity of the mouth by a layer of bone, but bulge backwards into it. The skull of the tadpole, from which that of the frog is developed, is cartilaginous, like that of *Scyliorhinus*. Subsequently this becomes considerably strengthened by the formation of bones. Some of these actually replace the cartilage, and are known as **cartilage-bones**, whilst others are plastered on to the surface. These latter are called **membrane-bones**, on account of the fact that their position is previously indicated by the presence of connective tissue membranes.

At its posterior end the skull is pierced by a large hole, known as the **foramen magnum**, through which passes the nerve-cord to establish continuity with the brain. The foramen magnum is bordered on each side by an **exoccipital** cartilage-bone, and above and below by cartilage. At the anterior end is another cartilage-bone, the **sphenethmoid**. The whole neurocranium is in the form of a box, narrowing towards its anterior end, near which a transverse partition separates the cranium from the cavity in front. The whole dorsal surface of the skull is covered by a pair of membrane-bones, the **frontoparietals**, extending from the sphenethmoid

to the exoccipitals, whilst along the ventral surface runs a dagger-shaped **parasphenoid**, the blade pointing in an anterior direction and the transverse portion of the hilt being extended to cover the floor of the auditory capsules.

The nasal capsules are continuous with the front end of the cranium, and consist mostly of cartilage, except for the anterior extension of the sphenethmoid beyond the limit of the cranium. The cavity of the sphenethmoid in the nasal region becomes divided by a vertical partition, termed

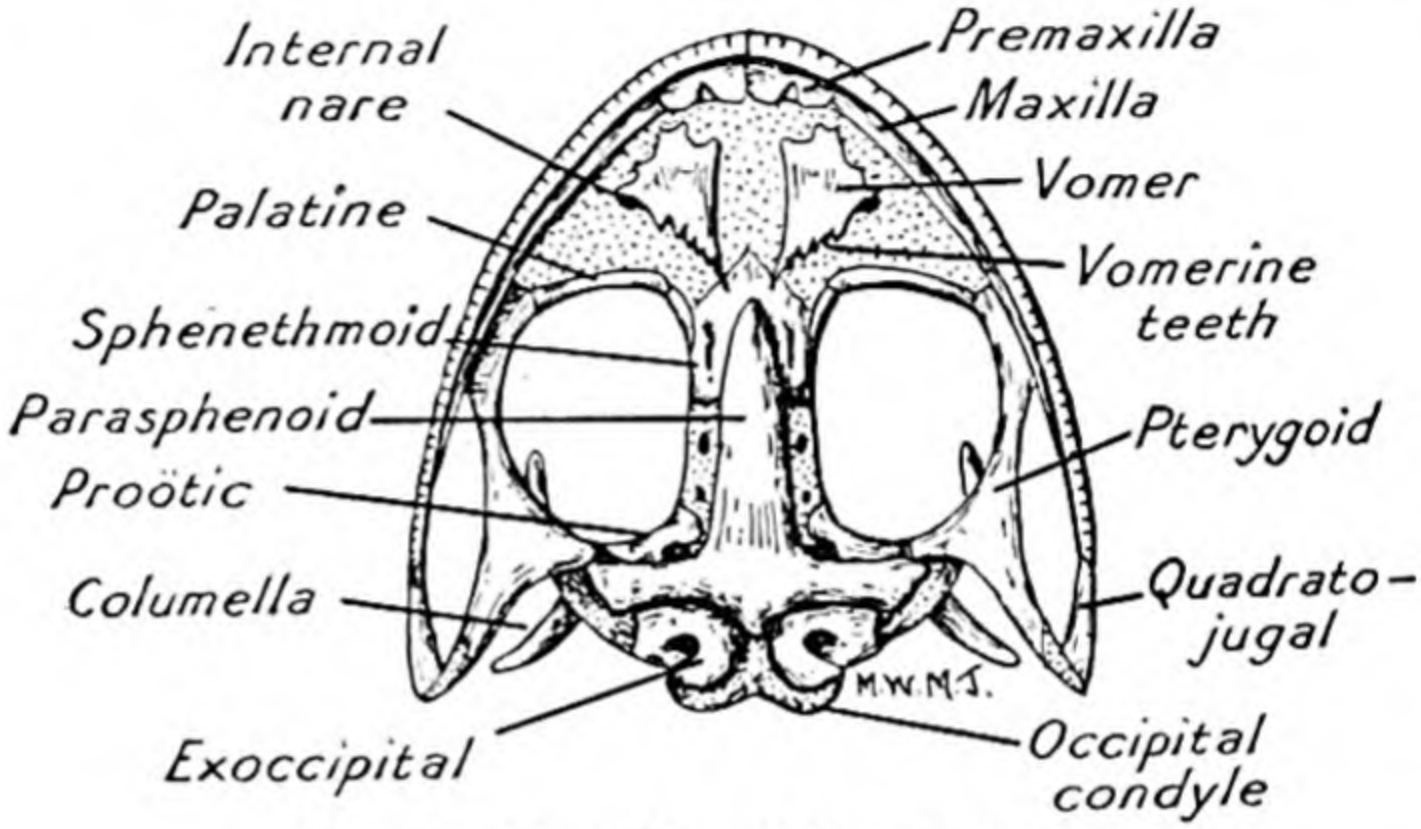


FIG. 79 – *Rana*. Ventral view of the skull.

the **mesethmoid**, into right and left halves. Each capsule is open below and above, for each external nare (nostril) leads by a tube into the nasal capsule of its own side, whilst below a tube passes from the nasal capsule into the mouth, into which it opens by an internal nare. Covering the dorsal surface of each capsule is a membrane-bone, known as the **nasal**, whilst the floor of each is protected by another membrane-bone – the **vomer**. Embedded in this latter is the cluster of vomerine teeth of its own side.

Continuous with the postero-lateral corners of the cranium are the auditory capsules, consisting mostly of cartilage. Each contains a somewhat subdivided cavity, known as the **cartilaginous labyrinth**, in which is embedded the internal ear, described in contrast as the **membranous labyrinth**. The anterior portion of each auditory capsule becomes ossified to form the **proötic** (therefore a cartilage-bone), and on to this is fixed a T-shaped membrane-bone, the **squamosal**, with the free limb of the T directed ventro-laterally. For communication to be established with the outside it is essential that at one point in each capsule bone shall be absent. This region is known as the **fenestra ovalis**, and across it a membrane is tightly stretched. This is separated by a short space from

the ear-drum, or tympanum, and a rod of bone connects these two membranes in order that vibrations may be transferred from one to the other, and hence ultimately to the ear. This bone is the **columella auris.**

Since the brain and sense-organs are thus enclosed within the neurocranium it follows that apertures, known as **foramina,** must be pierced in the lateral walls, especially of the cranium, to permit the passage of nerves to and from the brain, as well as allowing a supply of blood to reach this organ. The skull of the frog is too small for a detailed study of these foramina to be made here, but they are dealt with in the case of the skull of the dog (page 149).

The skeleton of the upper jaw consists essentially of an inner and outer series of paired bones. The **palatine,** a bone of mixed origin, is attached by a rod of cartilage to the hind end of the nasal capsules. To the posterior end of this cartilaginous rod, behind the palatine, is attached the foot of a Y-shaped **pterygoid,** with the arms of the Y directed backwards. The inner arm abuts on to the auditory capsule, whilst the outer runs ventrolaterally beneath, and parallel to the long limb of, the squamosal, from which it is separated by a rod of cartilage, known as the **quadrate,** continuous at its inner end with the auditory capsule. The outer series of membrane-bones comprising the upper jaw are the **premaxillae,** the **maxillae** and the **quadratojugals.** The premaxillae are a pair of small bones, plastered on to the anterior end of the nasal capsules, the two meeting in front in the middle line. Behind the premaxilla on each side is a long, slender maxilla. Anteriorly this is expanded dorsally to abut on to the nasal capsule, which thus assists in supporting it, whilst posteriorly it is connected by another bone, the quadratojugal, with the quadrate. The premaxillae and maxillae each bear a single row of teeth.

The lower jaw consists of two rods, each termed a **Meckel's cartilage** and joined anteriorly to the one of the opposite side by a ligament. At the anterior end a small portion of each cartilagenous rod has become ossified to form a small cartilage-bone, the **mento-meckelian.** Plastered on to the outer surface is a **dentary** membrane-bone, whilst on its inner face each Meckel's cartilage is almost completely covered by another membrane-bone, the **angulo-splenial.** Posteriorly each Meckel's cartilage articulates with the quadrate of its own side.

The remainder of the splanchnocranium (*i.e.* the skull other than the neurocranium) is constituted by the **hyoid** apparatus. This is a median plate, consisting almost entirely of cartilage, occurring in the floor of the mouth. The main bulk of this structure is termed the **body.** At the anterior end are two very long processes, known as **cornua,** which after running backwards for some distance parallel to the body, turn forwards and upwards to become attached to the sides of the auditory capsules. Two smaller posterior cornua project backwards, one on either side of the **larynx** (windpipe) and these are the only portions of the hyoid apparatus to become ossified.

The method of jaw suspension in the frog is known as **autostylic**, the quadrate being directly attached to the neurocranium, the columella auris (represented by the hyomandibula of *Scyliorhinus*) playing no part in this suspension.

(B) VERTEBRAL COLUMN. This consists of nine rings of bone, known as **vertebrae**, placed together end to end so as to form a bony tube to contain the spinal cord. At the posterior end is a long, tubular bone, known as the **urostyle**, articulating with the ninth vertebra and composed of a number of fused vertebrae. Each vertebra consists of a body, or **centrum**, situated beneath the spinal cord and giving off a **neural arch** on each side. These meet and fuse in the mid-dorsal line to enclose the nerve-cord. Each centrum is concave in front and convex behind, except the eighth, which is concave at both ends. At the line of junction of the two neural arches is formed a **neural spine**, in the nature of a ridge, whilst on each arch, except those of the first vertebra, is developed laterally a pair of **transverse processes**. These are especially large in the sacral (ninth) vertebra, for these articulate with the proximal ends of the ilia of the pelvic girdle. At the free end of each transverse process is a small pad of cartilage, representing a rib. The transverse processes themselves provide means of attachment for muscles. At the front and hind ends of each vertebra are special articulating surfaces, known as **zygapophyses**. The anterior zygapophyses are directed upwards and slightly inwards, whilst the posterior zyapophyses face downwards and slightly outwards. The posterior zygapophyses of each vertebra articulate with the anterior zygapophyses of the vertebra next behind, thus imparting flexibility to the vertebral column. Between every two successive vertebrae there is enclosed on each side an **intervertebral foramen**, through which emerges a spinal nerve. One such pair of apertures occurs a short distance behind the front end of the urostyle for the egress of the tenth spinal nerves. The first vertebra is somewhat modified, and is known as the **atlas**. It has no transverse processes, and articulates in front with the exoccipital condyles of the skull.

(C) PECTORAL GIRDLE AND FORE-LIMB. The pectoral girdle consists of an almost complete hoop of cartilage and bone, lying in the body-wall of the anterior region of the trunk and divisible into two identical halves in the mid-ventral line, where these two halves unite in a **symphysis**. Like the corresponding structure in the dogfish each, half of the pectoral girdle is divisible into a dorsal scapular and a ventral coracoid region, but in the frog the original cartilage has become largely replaced by bone (therefore cartilage-bone), whilst there is one pair of membrane-bones developed, the clavicles. The most dorsal region consists of a large, broad plate on each side, known as the **supra-scapula**, and consisting almost entirely of calcified cartilage. Laterally the supra-scapula is connected with a smaller cartilage-bone, the **scapula**, an anterior projection from which forms the **acromion process**. Ventral to

the scapula lies the coracoid region, composed of cartilage and bone and attached laterally to the scapula. The **coracoid** bone itself is situated posteriorly and is separated from a slender membrane-bone, the **clavicle,** in front by a **coracoid fontanelle**. Lying along the clavicle and posterior to it is a strip of calcified cartilage, the **precoracoid**, whilst this is continued in a posterior direction to form the **epicoracoid** along the inner

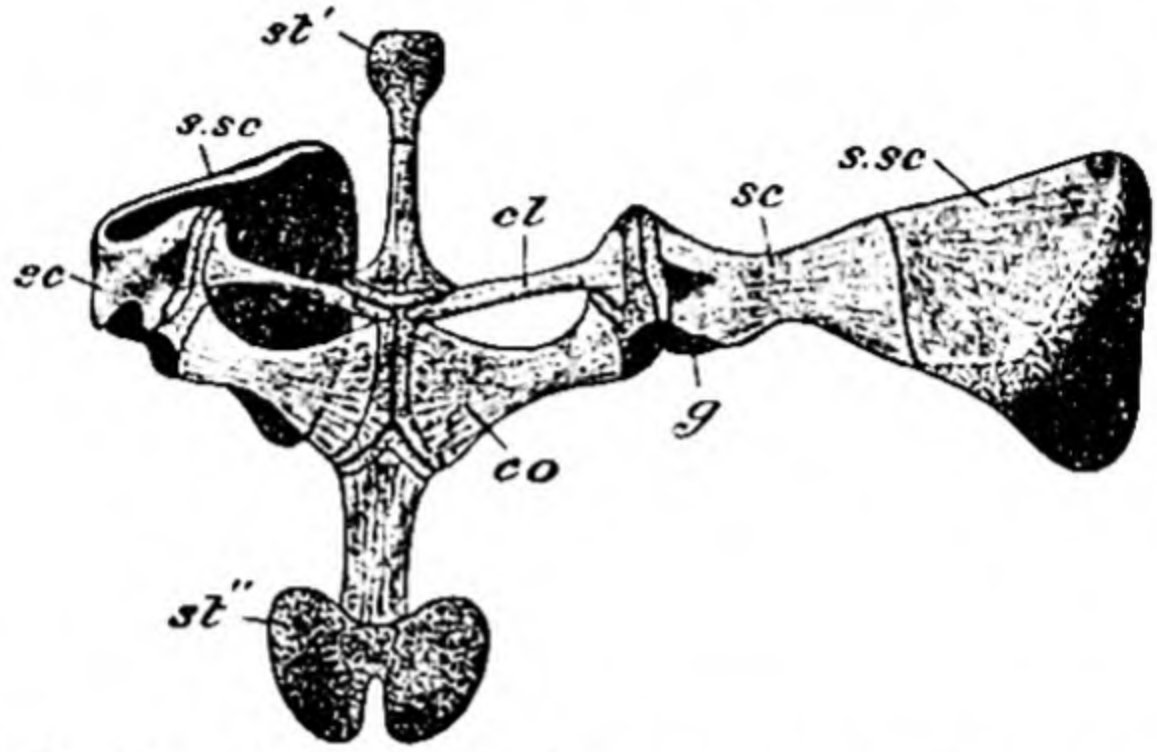


FIG. 80 – *Rana*. Pectoral girdle, from ventral side. (From 'Atlas of Practical Elementary Zootomy', by G. B. Howes. Macmillan.) *cl.*, clavicle; *co.*, coracoid; *g.*, glenoid facet; *sc.*, scapula; *s.sc.*, supra-scapula; *st'.*, episternum; *st".*, xiphoid cartilage.

margin of the coracoid itself. The two halves of the girdle become continuous in the mid ventral line, a symphysis being established between the pre- and epi-coracoids of the two sides. Posteriorly there is attached to the epicoracoids a median cartilage-bone, known as the **xiphisternum**, continuous with an expanded **xiphoid cartilage**. In front the fused precoracoids have attached to them a cartilage-bone, the **omosternum**, bearing at its free extremity a small plate of cartilage called the **episternum**. Enclosed between the scapula and the coracoid bones on each side is a depression. This is the **glenoid cavity**, into which fits the head of the first bone of the fore-limb.

The bone of the upper arm is the **humerus**. This is chiefly characterised by a **deltoid ridge** along its inner side, whilst the main shaft of the bone is swollen at each end. The proximal swelling forms the **head**, set in the glenoid cavity, whilst the distal swelling is known as the **trochlea**, and serves for the reception of the bone of the forearm. This latter is the **radio-ulna**, so-called on account of its double nature, the radius and ulna being separate bones in mammals. The radial portion of this composite bone in the frog lies on the inner side of the limb, though twisting slightly to lie above the ulnar portion proximally. There is a heel-like process on the radio-ulna, projecting backwards beyond the region of articulation with the humerus, and this is known as the elbow, or **olecranon**

process. The wrist, or **carpus**, is made up of a number of **carpals**, arranged in two rows. The proximal row consists of three carpals, named the radiale, intermedium and ulnare, whilst the distal row in the adult frog also contains three such bones, five being present in early stages of development and subsequent fusion taking place. There are only four fully-formed digits, each consisting of a basal **metacarpal**, articulating with a number of **phalanges**. The first digit, known as the pollex, consists of a metacarpal only, whilst digits II, III, IV and V bear respectively 2, 2, 3 and 3 phalanges.

(D) PELVIC GIRDLE AND HIND-LIMB. This, like the pectoral girdle, is made up of two halves, fused together ventrally to form between them an almost complete hoop of bone. But, whereas the pectoral girdle was placed almost at right angles to the vertebral column, the pelvic girdle is so set as to lie almost parallel to it. Thus a very rigid fulcrum is formed for the movements of the powerful hind legs, whether in leaping or swimming. On the outer side of each half is a cavity, known as the **acetabulum**, for the reception of the head of the bone of the thigh. Situated above this is the **ilium**, running forwards to become attached to the transverse process of the sacrum of its own side. The two ilia meet posteriorly and fuse to form an **iliac symphysis**. This iliac region corresponds to the scapular region of the pectoral girdle. The portion of the pelvic girdle lying below the acetabulum is termed the **ischiopubic** region, and corresponds to the coracoid region of the pectoral girdle. It is made up of a cartilaginous **pubis**, forming the anterior portion of the girdle, thus corresponding to the precoracoid of the pectoral girdle. The two pubes become completely united in a **pubic symphysis**. The posterior part of this ventral region is made up of the **ischium**, corresponding therefore to the coracoid proper. The two ischia also become completely fused. Between the pubis and the ischium lies a piece of calcified cartilage, known as the **post-pubic cartilage**. This cartilage and the three bones mentioned all play a part in the enclosing of the acetabulum.

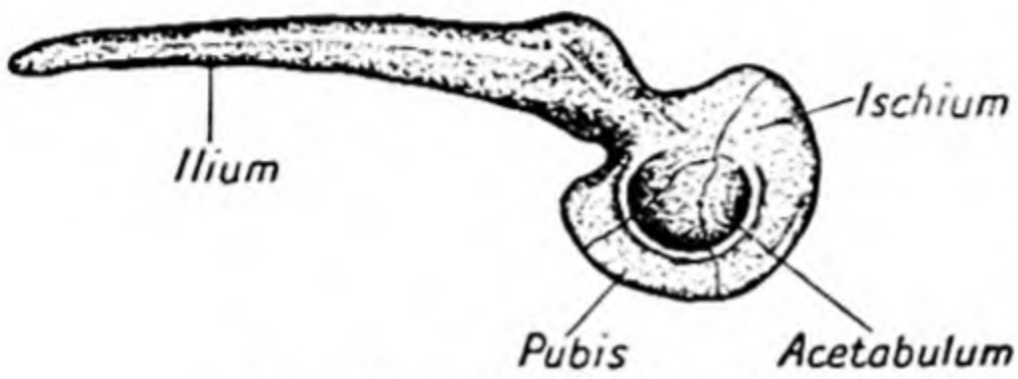


FIG. 81 – *Rana*. Half-pelvis.

The thigh-bone, or **femur**, is long and very slightly curved. Proximally it fits into the acetabulum, and from this head end projects a small process, known as the trochanter. The bone of the lower leg is the **tibio-fibula**, of double nature, as indicated by a groove running almost throughout its whole length. In many higher animals the two components of this bone are completely separated. In the frog the tibial portion is pre-axial and the fibular portion postaxial in position. The fusion of the

two bones maintains the limb at the best angle to obtain maximum thrust when the animal leaps or swims. It is expanded at both ends, and the lower end articulates with the ankle, or **tarsus**. There are only two

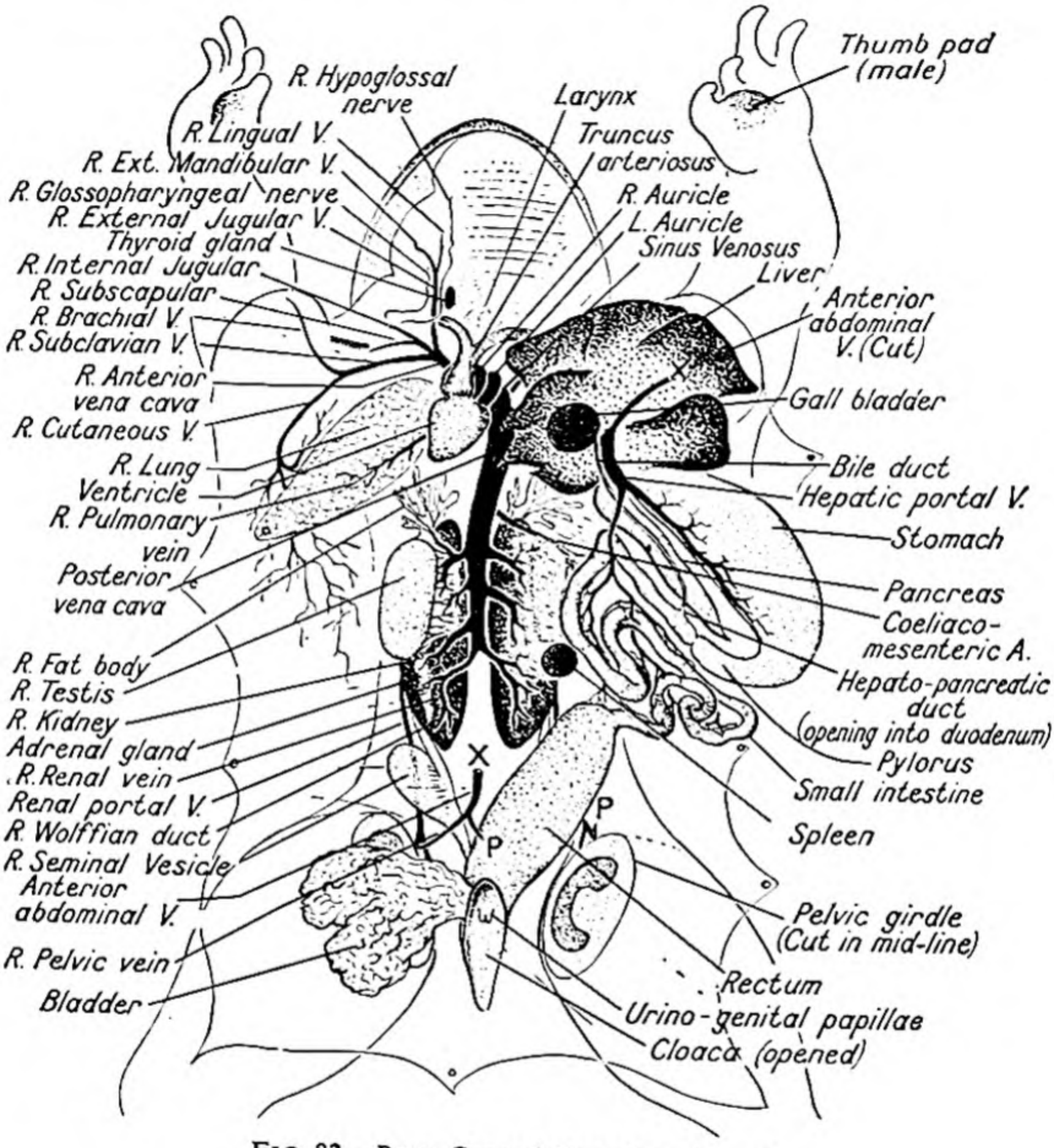


FIG. 82 – *Rana*. General dissection of a male.

proximal **tarsals**, the astragalus (on the tibial side) and the calcaneum (on the fibular side). These are widely separated in the middle, but united at the ends, whilst both are considerably elongated. There are two small distal tarsals, articulating with six **metatarsals**, which form the instep, and with which the **phalanges** of the toes articulate. On the inner side of the first toe, or hallux, lies a small toe, the calcar, consisting of a short metatarsal and one phalanx, the hallux itself bearing two phalanges.

Digits III to VI (counting the hallux as II) possess respectively 2, 3, 4 and 3 phalanges. The entire structure of the pelvic region and hind-limbs shows marked adaptation to the frog's habit of jumping.

Internal Anatomy

Though all the internal organs of the frog function as one collective whole to effect its life-processes, it is convenient for purposes of description to segregate them into a number of groups. All the organs included in each such group are concerned primarily with some one particular function, and together they comprise a system. The various systems of the frog will therefore be dealt with in detail individually.

Alimentary System

The alimentary system consists of a tube, leading from mouth to cloaca, and through which all the food passes. It is considerably longer than the body of the frog, and is therefore coiled. Arising from, and functioning in conjunction with, this tube is a number of other organs, which will therefore be included in the description of the alimentary system. In the mouth, or buccal cavity, of the frog is contained a long, folded tongue. This is peculiar in that it is attached at the front of the mouth, and when at rest is directed backwards. It is forked and sticky at the tip, and may be shot out rapidly to effect the capture of insects on

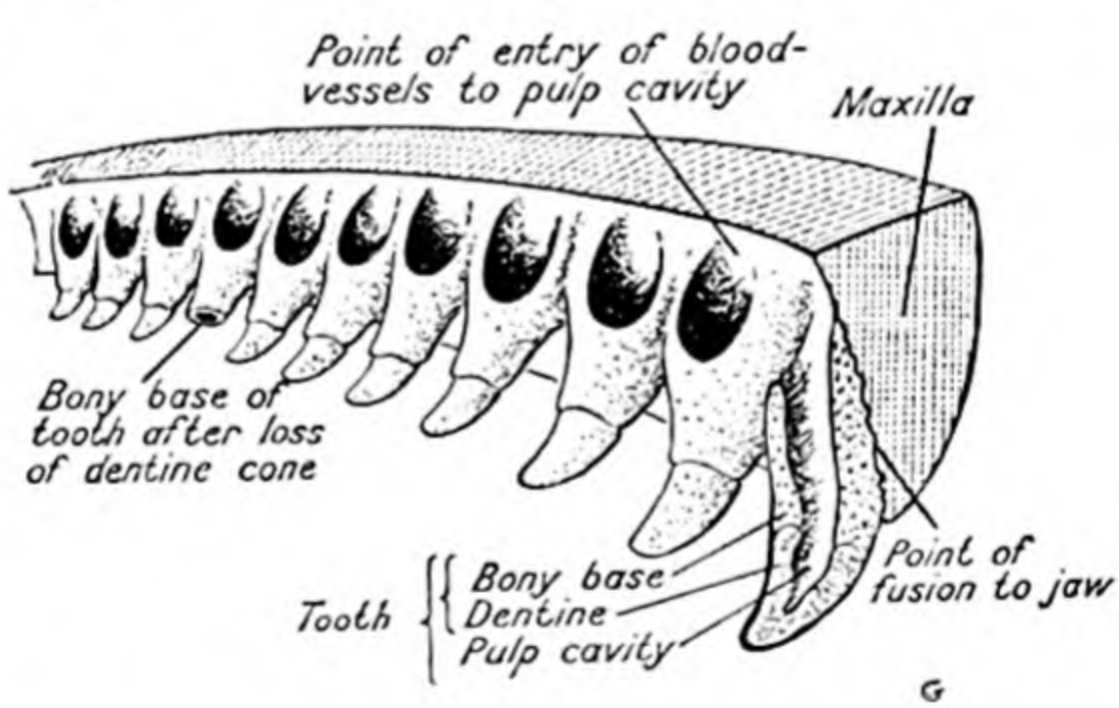


FIG. 83 – Teeth of frog, seen from inside the mouth.

which the frog feeds. The frog's food is not confined to insects, for it includes earth-worms, slugs and 'grubs' in its diet. Prey is swallowed whole and killed by the acids of the stomach, where it remains for up to three days. The upper jaw is fringed with a single row of teeth. Each of these is a conical structure, resembling the placoid scales of the dog-fish but fused to the bone of the jaw. It consists of a hollow mass of dentine, covered by a cap of enamel. Into the dentine extends a vascularised pulp-cavity. As these teeth wear out they are replaced

throughout life by new ones. On the roof of the mouth is a pair of patches of vomerine teeth, to the outer side of each of which opens an internal nare. The posterior extremity of the mouth is known as the pharynx, and into it opens a pair of **Eustachian tubes**, one communicating with the inner side of each tympanum. These Eustachian tubes are extended laterally to form the **vocal sacs**, which largely facilitate the croaking sounds emitted in the breeding season. In the floor of the pharynx is a slit-like aperture, known as the **glottis**, which leads to the larynx. During swallowing this glottis can be closed, and thus food is prevented from passing into the larynx. From the pharynx the alimentary canal is continued backwards in the form of a narrow oesophagus. This leads into a wider stomach, somewhat constricted at either end. At its distal end this constriction is known as the **pylorus** and leads into a duodenum. The opening between the stomach and the duodenum can be closed by means of a sphincter muscle (see page 90). The duodenum is narrow, and turns forwards so as to run parallel to the stomach. It leads into the narrow, coiled intestine, which widens at its posterior end to form the rectum. This is short, and the alimentary canal now terminates by opening to the exterior via the cloaca. On to the ventral surface of the hind end of the rectum opens the urinary bladder. As well as the simple tube already described a number of glands go to comprise the alimentary system. A **gland** is an organ concerned in the elaboration of some definite chemical substance of use to the body. The largest of these glands is the liver. This is attached near the base of the oesophagus, and consists of a large left lobe, a slightly smaller right lobe and a small, median lobe. Between the right and left lobes occurs a structure, usually green in colour, known as the gall-bladder. Leading from this to the duodenum is a narrow tube known as the bile-duct. Though this is not easily seen in dissection it can often be observed by first squeezing the gall-bladder between the thumb and finger, when the green bile forced into this duct renders it conspicuous. Between the stomach and the duodenum lies an elongated, yellowish gland, termed the pancreas. This is in communication with the duodenum by way of the hepato-pancreatic duct, which passes through it.

The process of digestion, accommodated by the alimentary system, is fully described in Chapter 23, with reference principally to the mammal.

Vascular System

The main organ of the vascular system is the heart, acting as a pump to keep the blood in motion. The blood is conveyed about the body in vessels, known as arteries and veins. An **artery** is a blood-vessel which carries blood away from the heart, whereas a **vein** carries blood towards the heart. As will be seen later it is not true to say that an artery carries the oxygenated blood and a vein the de-oxygenated.

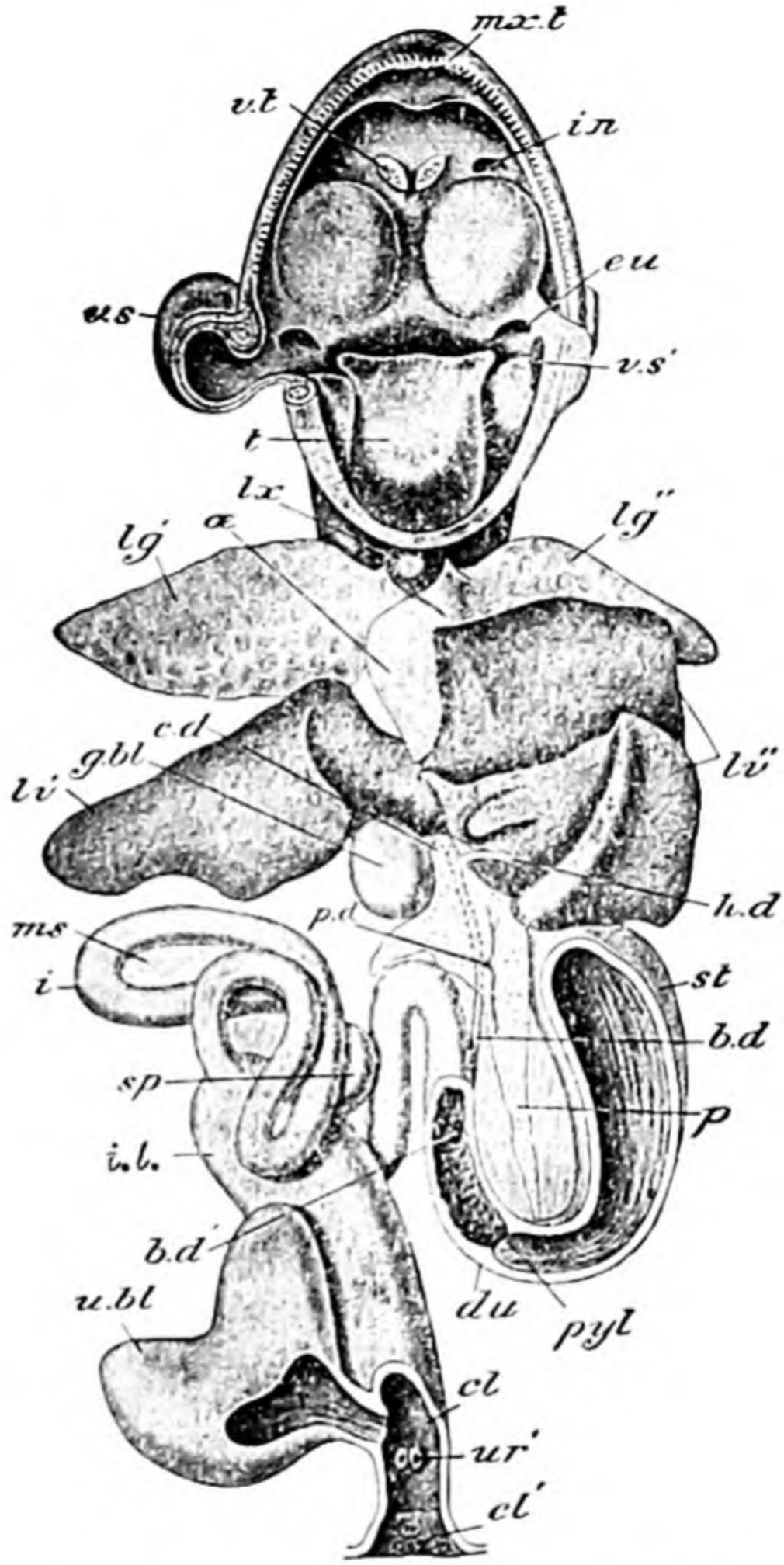


FIG. 84 – *Rana*. Alimentary canal and its diverticula. (From 'Atlas of Practical Elementary Zootomy', by G. B. Howes. Macmillan.)

b.d., so-called bile duct; *b.d'.*, aperture of same; *c.d.*, cystic duct; *cl.*, cloaca; *cl'.*, aperture of same; *du.*, duodenum; *eu.*, Eustachian aperture; *g.bl.*, gall bladder; *h.d.*, hepatic duct; *i.*, intestine; *i.l.*, rectum; *i.n.*, internal nare; *lg'.*, right lung; *lg".*, left lung; *lv'.*, liver, right lobe; *lv".*, liver, left lobe; *lx.*, larynx; *ms.*, mesentery; *mx.t.*, premaxillo-maxillary teeth; *p.*, pancreas; *p.d.*, pancreatic duct; *pyl.*, pylorus; *sp.*, spleen; *st.*, stomach; *t.*, tongue; *u.bl.*, bladder; *uri.*, aperture of Wolffian duct; *v.s.*, right vocal sac; *v.s'.*, orifice of left vocal sac; *v.t.*, vomerine tooth; *oe.*, oesophagus.

(A) HEART. The heart is divided into three main chambers, known respectively as the **right auricle**, the **left auricle** and the **ventricle**. The latter is a thick-walled structure lying posterior to the two smaller, thin-walled auricles, the right of which is larger than the left. Lying on the dorsal side of the heart is a reservoir, known as the **sinus venosus**, into which is drained blood from all parts of the body except the lungs. Lying ventrally across the face of the heart, of which it should be regarded as a part, is a thick-walled, muscular tube, called the **truncus arteriosus**. This opens into the ventricle and provides the sole means of egress of blood from the heart. The whole heart is enclosed in a portion of the coelom,

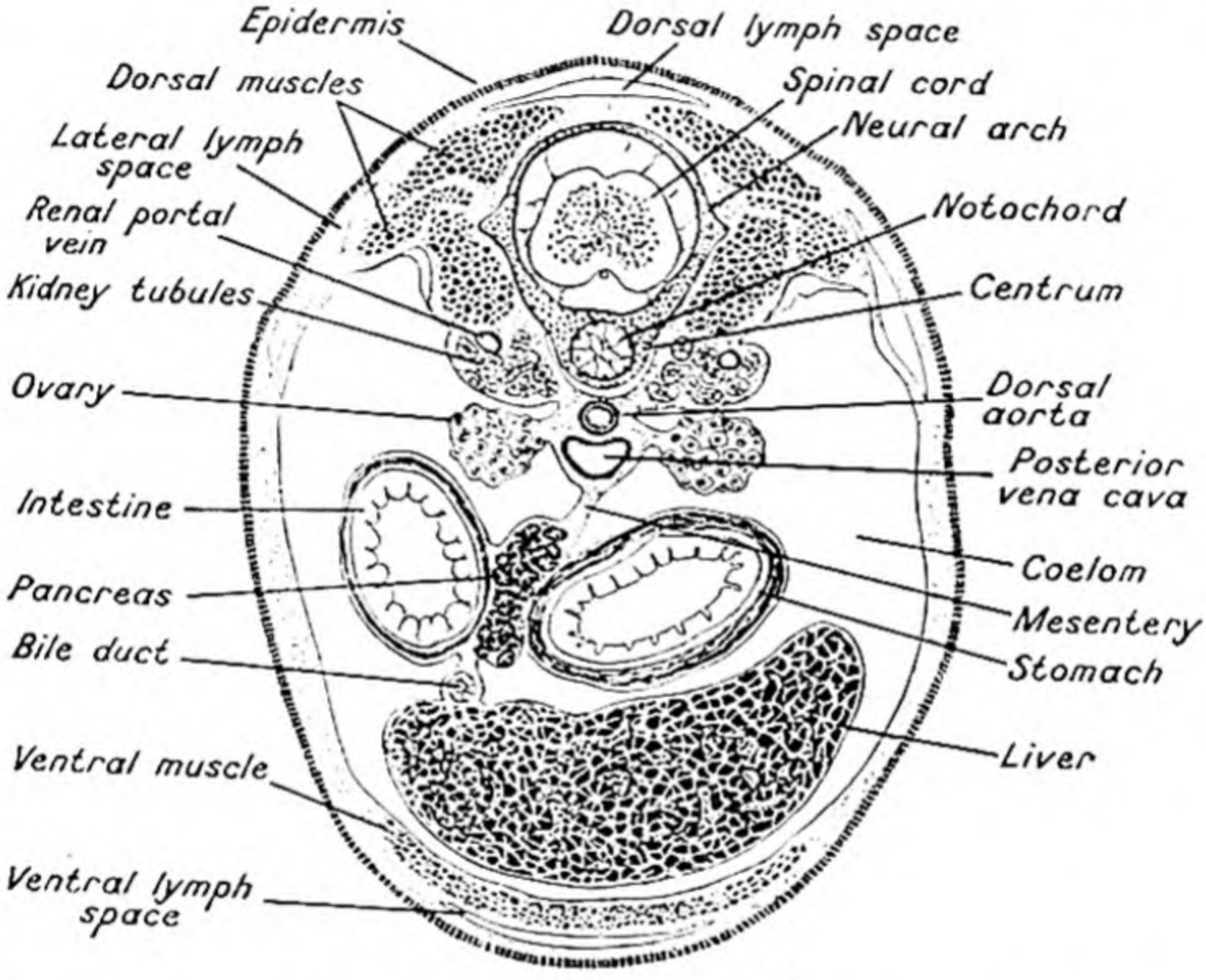


FIG. 85 – *Rana*. Transverse section of the trunk region of a young frog, illustrating basic vertebrate structure.

walled off from the general peritoneal cavity and known as the **pericardial cavity**. The openings between the various chambers of the heart and the vessels immediately connected with them are guarded by **valves** formed by folds in the lining of the heart. Two small flaps of skin comprise the sino-auricular valves between the sinus venosus and the right auricle, into which it opens, whilst each auriculo-ventricular aperture is similarly guarded. These latter valves are held in position by fine cords, known as **chordae tendineae**, attached to the wall of the ventricle. There is no direct communication between the right and left auricles. Three semi-lunar valves occur at the base of the truncus arteriosus, whereas

near the distal end of this organ three more similar valves divide the truncus into a **conus arteriosus** (proximal) and a short **ventral aorta,** corresponding to the structures of the same name associated with the heart in *Scyliorhinus*. Lying in the conus is a twisted fold of skin, constituting the **spiral valve.**

(B) ACTION OF THE HEART. Blood from the sinus venosus is conveyed to the right auricle, whereas the left auricle receives blood from the lungs via the pulmonary vein.

The traditional explanation of the mechanism of the frog's heart was based on the assumption that blood in the left auricle was highly oxygenated and that in the right largely de-oxygenated. Furthermore,

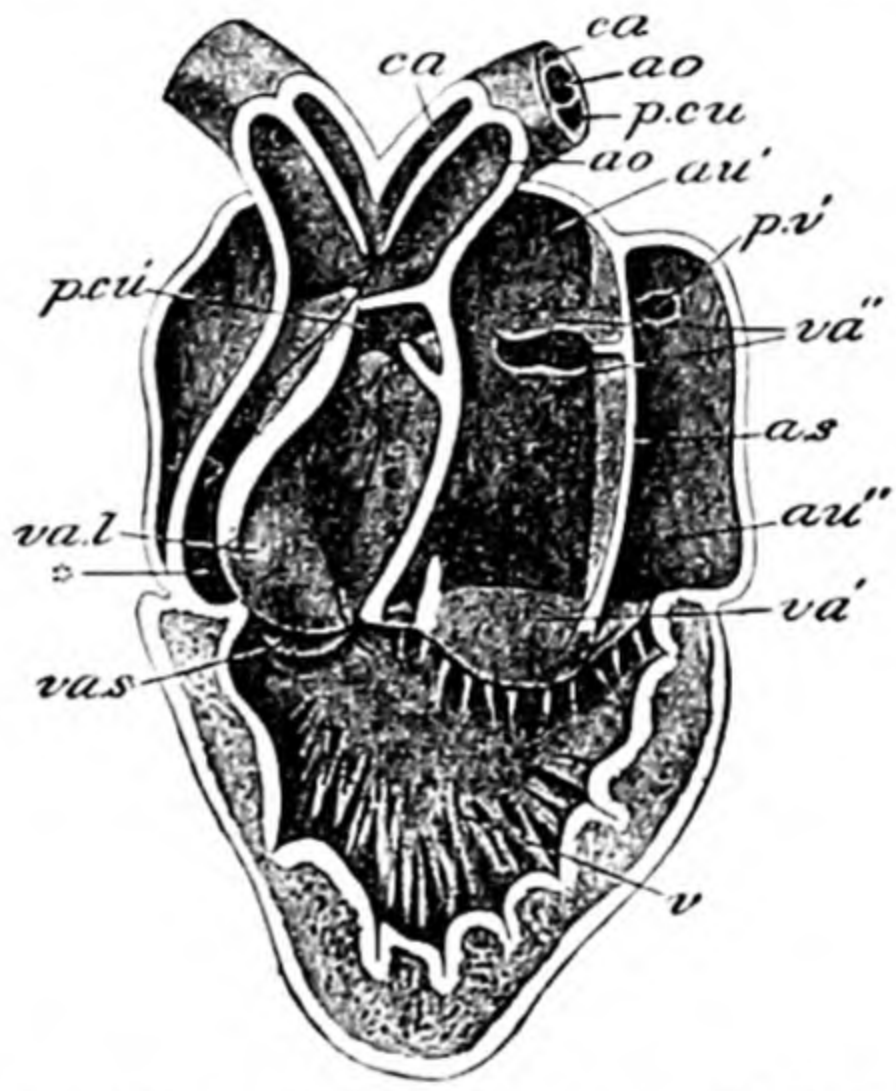


FIG. 86 – *Rana*. Heart, opened from ventral surface. (From 'Atlas of Practical Elementary Zootomy', by G. B. Howes. Macmillan.)
a.s., interauricular septum; *ao.*, systemic arch; *au'.*, right auricle; *au".*, left auricle; *ca.*, carotid arch; *p.cu.*, pulmocutaneous arch; *p.cu'.*, pulmocutaneous orifice; *p.v'.*, orifice of pulmonary veins; *v.*, ventricle; *va'.*, dorsal auriculo-ventricular valve; *va".*, sinu-auricular valves; *va.l.*, spiral valve of truncus; *va.s.*, semilunar valve.

accounts of the subsequent behaviour of the blood have assumed that the streams of oxygenated and de-oxygenated blood are passed through the remainder of the heart and eventually distributed, with only very restricted mixing of the two types of blood. It was explained that such mixing would not take place in the ventricle, since blood is present there for so short a time, and in any case is a fairly viscous liquid. In addition, its movement is further impeded by tongue-like projections – *columnae*

carnae – from the wall of the ventricle. Upon the contraction of the ventricle the de-oxygenated blood was held to pass first up the truncus, since it apparently lay in the right half of the ventricle. This de-oxygenated blood was presumably directed into the pulmocutaneous arches, to reach

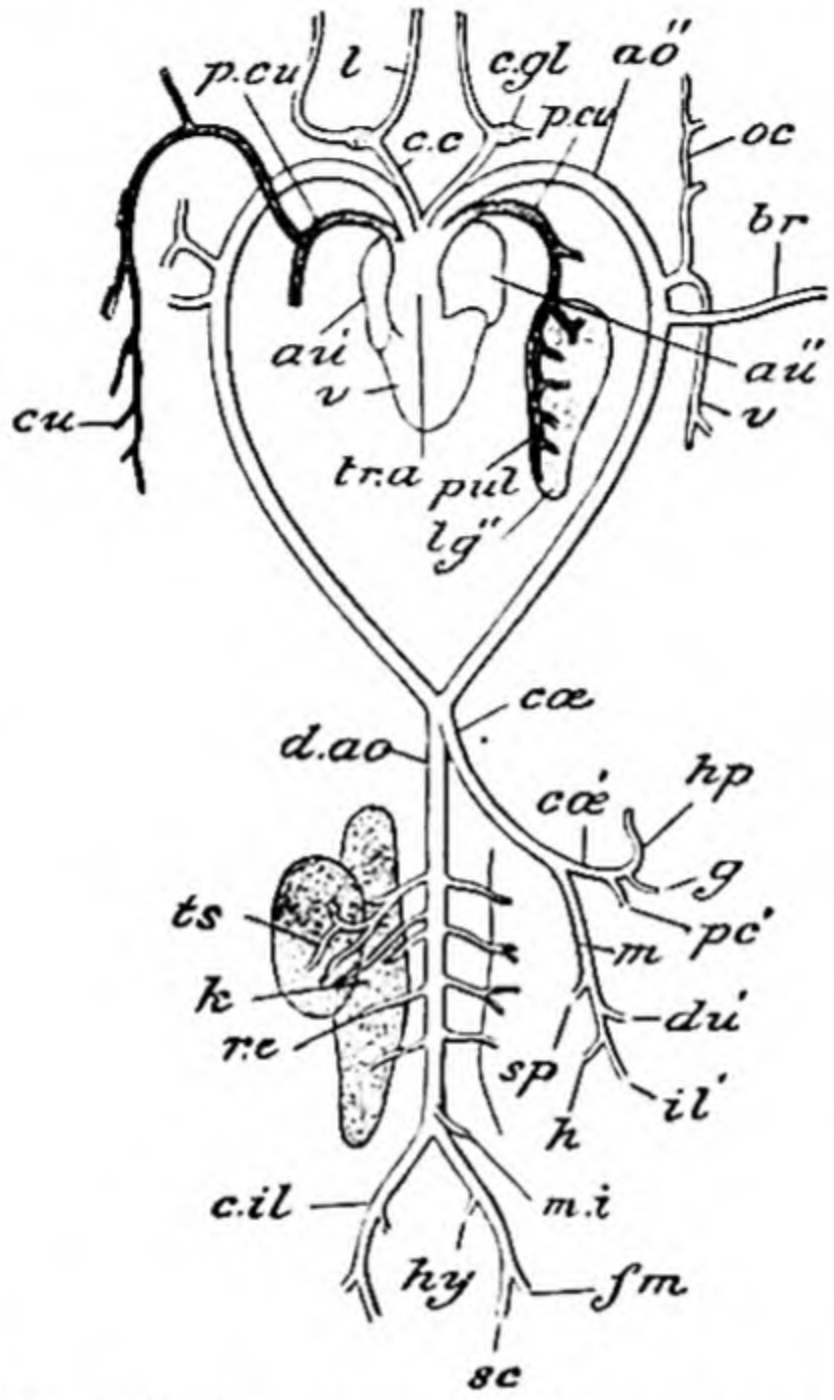


FIG. 87 – *Rana*. Dissection of the arterial system, as seen after the removal of the alimentary canal and liver. (From 'Atlas of Practical Elementary Zootomy', by G. B. Howes. Macmillan.) *ao''*., left aortic arch; *br*., brachial artery; *c.c*., common carotid artery; *c.gl*., carotid 'gland' (plexus); *c. l*., common iliac artery; *coe*., coeliaco-mesenteric artery; *coe'*., coeliac artery; *cu*., cutaneous branch of pulmonary artery; *d.ao*., dorsal aorta; *du'*., duodenal artery; *fm*., femoral artery; *g*., gastric artery; *hp*., hepatic artery; *hy*., hypogastric artery (to bladder); *il*., ileal artery; *l*., lingual artery; *m*., anterior mesenteric artery; *m.i*., posterior mesenteric artery; *oc*., occipital artery; *pc'*., pancreatic artery; *p.cu*., pulmocutaneous arch; *pul*., pulmonary artery; *re*., renal artery; *sc*., sciatic artery; *sp*., splenic artery; *tr.a*., truncus arteriosus; *ts*., testicular artery; *v*., vertebral artery.

the lungs and skin for oxygenation. Mixed blood followed, to be distributed along the systemic arches, and finally the blood rich in oxygen was conveyed along the carotid arches to the head.

Experimental evidence, however, has done much to invalidate this hypothesis. Vandervael investigated the distribution of Indian ink

particles by illumination of the heart from beneath. He found that, wherever the particles were introduced, they apparently found their way equally into all channels leading from the heart. Objections to the technique on the grounds of the possible effect of the inevitable heat on the action of the heart have been overcome by the later work of G. E. H. Foxon, using a radio-opaque medium, *thorotrast*. This may be introduced either into the sinus venosus or into the pulmonary veins. Serial radiographs made subsequently showed again that the medium was equally distributed along all exits from the heart. Furthermore, cases of individual frogs with deformed hearts, where the separation of the two streams could not possibly have been effected, have been reported. Yet such frogs had apparently been capable of a normal life.

More recent investigations, in which minute quantities of a suitable dye were employed, tend to suggest that the truth lies somewhere between the classical hypothesis and the one elaborated as a result of Foxon's work. It is suggested that there is *some* degree of separation maintained between the two streams of blood, the one from the left auricle and the other from the right, but that these two streams pass *simultaneously* up the truncus, and not successively, as was demanded by the classical hypothesis. Certainly the pulse waves in all three pairs of arches are simultaneous. This maintained separation may be aided by the spiral valve. The arches into which the respective streams of blood enter would appear to depend upon the positional relationships between these streams and the locations of the exits of the respective arches at the distal end of the truncus. Thus, blood from the right auricle is held to pass principally into the pulmo-cutaneous and left systematic arches, and blood from the left auricle into the remainder. Functionally, the importance of any mixing which may occur is reduced by the fact that blood returning to the sinus venosus is itself reasonably well oxygenated, much of it having come from the skin and the lining of the buccal cavity, which are important respiratory surfaces.

(C) ARTERIAL SYSTEM. The divisions of the truncus arteriosus have already been referred to. The carotid arch soon divides into a carotid artery and a lingual artery (to the tongue). Near the junction is a carotid gland, referred to again on page 138. Shortly after its origin each pulmo-cutaneous arch divides to form a **pulmonary** artery to the lung of its own side and a **cutaneous** artery to the skin. From the outer side of each systemic arch during its passage backwards arises a **subclavian** artery to the fore-limb, whilst several important arteries are given off from the dorsal aorta. Immediately behind the junction of the two systemic arches a **coeliaco-mesenteric** artery emerges from the ventral surface of the dorsal aorta to supply the gut. It becomes further subdivided into a hepatic (to the liver), a coeliac and an anterior mesenteric, supplying between them the spleen and the anterior part of the gut. Farther back a number of paired **renal** arteries run to the kidneys, whilst a **spermatic** or

ovarian artery arises, in male and female respectively, to supply each testis or ovary. Behind these a median **posterior mesenteric** arises to carry blood to the intestinal region. At its posterior end the dorsal aorta forks to form two **iliac** arteries, one running in either leg.

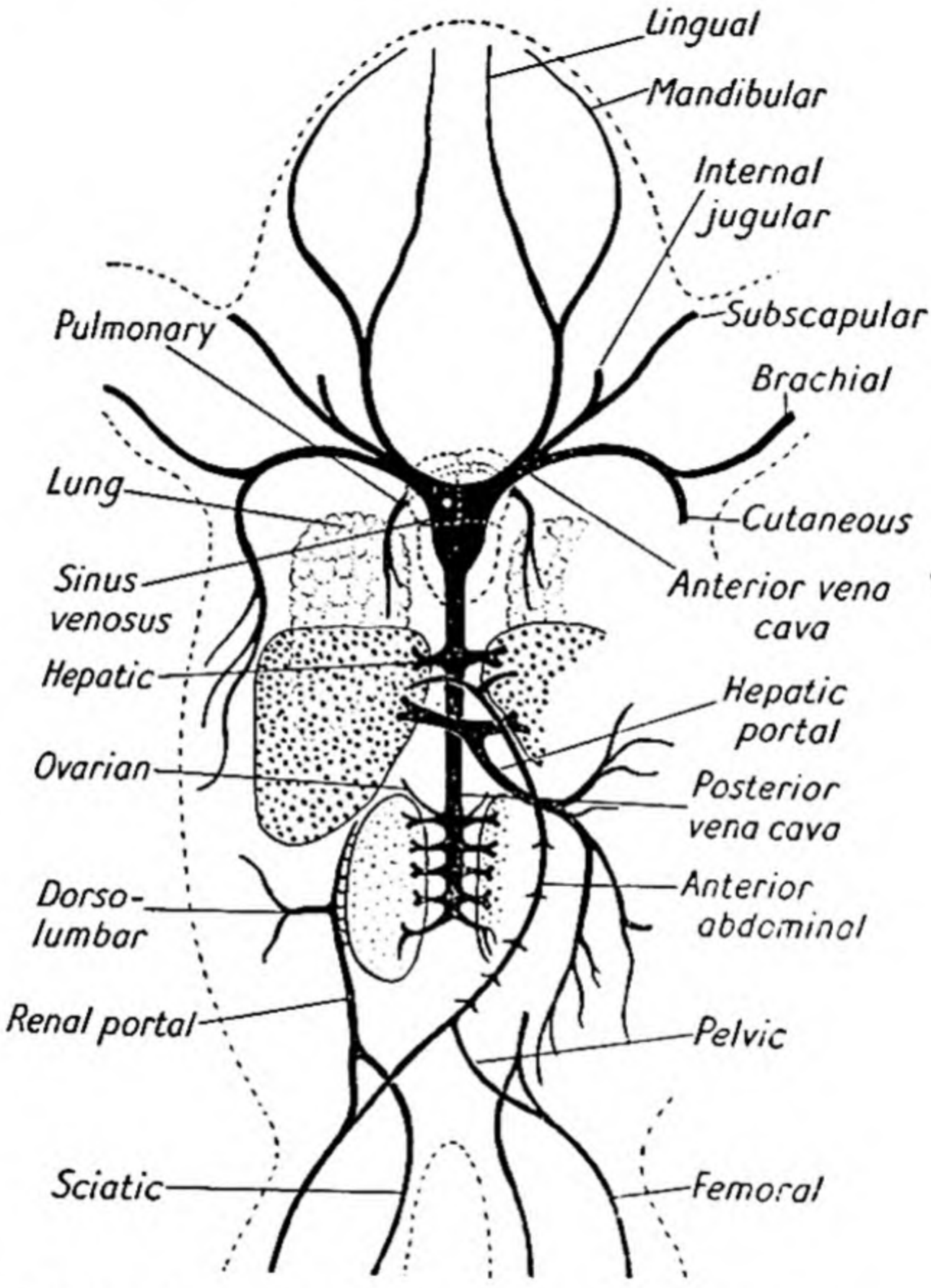


FIG. 88 – *Rana*. Diagram to show the general Venous System.

(D) VENOUS SYSTEM. Blood is returned from all parts of the body, except the lungs, by three great veins into the sinus venosus. The three veins in question are the **posterior vena cava** and a right and left **anterior vena cava**. Each anterior vena cava is formed by the union of three veins, known respectively (from in front backwards) as the external jugular, the innominate and the subclavian, each of which receives blood from two smaller veins; thus a total of six vessels empty blood into the anterior

vena cava. These branches (from in front backwards) are the lingual, returning blood from the tongue, the mandibular from the lower jaw, the internal jugular from the brain, the subscapular from the shoulder region, the brachial from the arm and the cutaneous from the skin. The posterior vena cava is a median vessel, lying in close association with the dorsal aorta. It receives two large hepatic veins from the liver, whilst posteriorly it arises as a number of paired renal veins, receiving blood from the kidneys, as well as the spermatic or ovarian from the reproductive organs of male and female respectively. There are two important sets of vessels to be considered in connexion with the venous system of the frog, comprising respectively the **hepatic portal** and **renal portal systems**. A portal vein is defined on page 96. The **hepatic portal** vein is a single structure, commencing as capillaries in the wall of the gut and terminating, again in the form of capillaries, in the tissues of the liver, where much of the carbohydrate material absorbed from the intestine is converted into glycogen and stored. There is a pair of **renal portal** veins, each of composite nature. Running from each hind leg is a femoral and a sciatic vein. These unite at the base of the trunk to form a renal portal vein, passing up along the outer edge of the kidney of its own side and penetrating this organ to break up into capillaries. Arising from each femoral vein and passing antero-ventrally is a pelvic vein, running ventral to the sciatic of its own side. The pelvic veins unite in the mid-ventral line in the body-wall and pass forwards as the **anterior abdominal** vein. When this reaches almost the level of the fore-limbs it leaves the body-wall and penetrates the liver, where it breaks up before continuing its journey to the heart, so that the anterior abdominal vein comprises part of the hepatic portal system.

Blood is returned to the left auricle from the lungs by a pair of **pulmonary** veins, which unite to form a common vessel just before entering the heart.

(E) THE PRINCIPLE OF BLOOD CIRCULATION. Every part of the body must be supplied with blood to facilitate both nutrition and respiration. It is therefore apparent that every such part of the body must be reached by a vein so that the blood, having given up its food and oxygen, may be conveyed away. When an artery reaches the organ it is destined to supply it fragments, the branches becoming progressively finer and more thin-walled until they eventually become designated as **capillaries**. From these the blood does not escape, but oxygen and liquid food diffuse into the tissues. The actual capillaries of the arteries are continuous with those of the veins. These latter join one another to give rise to progressively larger vessels until eventually a vein, running back to the heart, liver or kidneys, is formed. Thus the blood-system of the frog is described as closed, for the cells of the blood, including principally the red colouring-matter, never escape from the vessels in which they are carried, food and oxygen reaching the tissues by diffusion through

the walls of the capillaries. The blood thus partially exhausted is conveyed onwards, finally to reach the heart and be passed to lungs or intestine for fresh supplies. This closed type of blood-vascular system is characteristic of all the Chordata and many Invertebrata – e.g., the Annelida – and is to be contrasted with the open type found in the Arthropoda, where the tissues are actually bathed in blood.

The plan of blood-circulation in the frog is as follows. Mixed oxygenated and de-oxygenated blood leaves the ventricle by a common channel to be supplied to the various organs of the body, including the lungs and skin, to which passes blood for oxygenation. Blood from the lungs is returned to the left auricle, whilst that from the remaining organs of the body reaches the right auricle through the sinus venosus. These facts are summarised in Fig. 89.

Lymphatic System

It will be remembered that the tissues are bathed, not in blood itself, but in a nutrient fluid which exudes through the walls of the capillaries. This fluid is known as **lymph**. It comes to lie in small lymph-vessels, several of which may join to form a lymph-sac. Some of these are contractile and are known as lymph-hearts, which pump the lymph back into the great veins of the body.

Thus there is one pair of lymph-hearts near the urostyle, opening into the femoral veins, whilst a pair below the scapulae communicate with the subscapular veins.

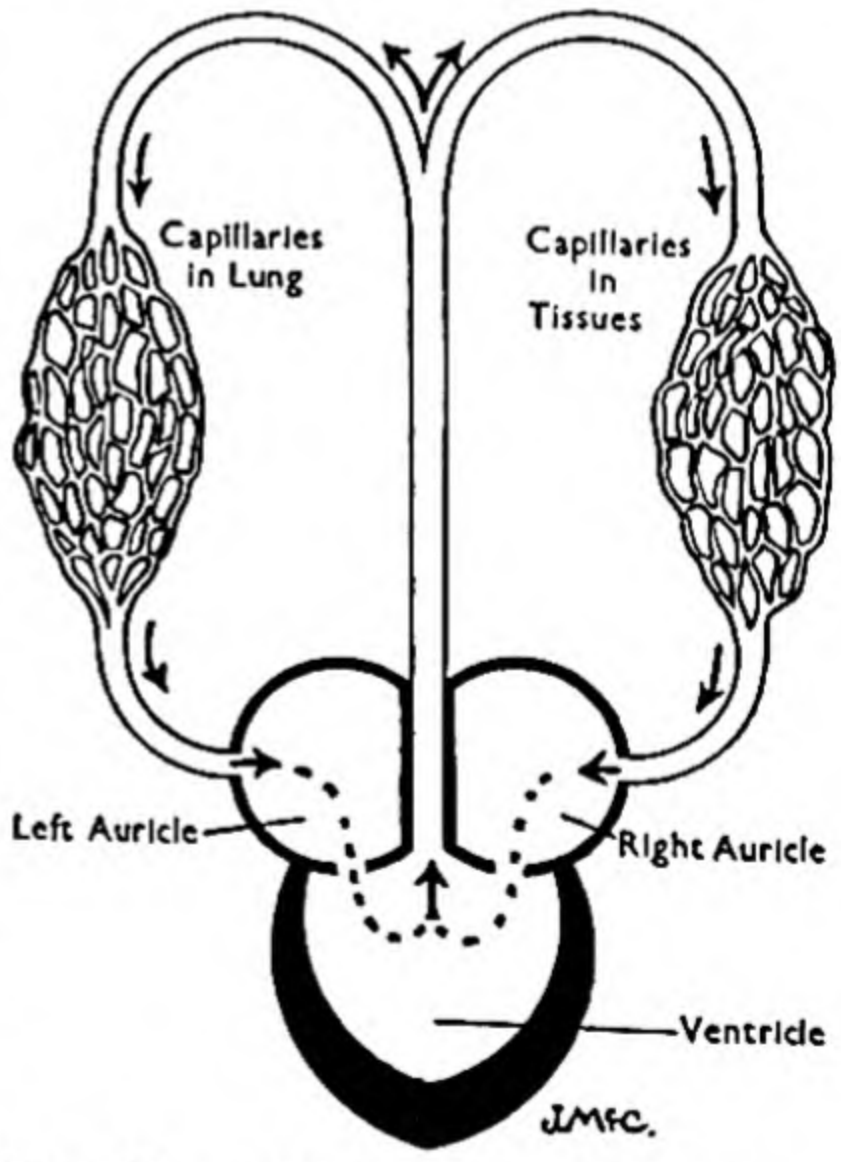


FIG. 89 – *Rana*. Diagram to illustrate the course of the circulation of the blood.

Respiratory System

It has already been pointed out that the frog uses its skin to a considerable extent for respiratory purposes. On this account it is kept moist to facilitate gaseous exchange when the animal is on land, whereas when submerged for long periods it relies exclusively on the skin for effecting respiration. On land the frog uses the thin lining of its buccal cavity and pharynx for gaseous exchange, as well as a pair of lungs. Leading from the ventral side of the oesophagus, via a slit-like opening, termed the **glottis**, is a

larynx, from which arises a pair of very short **bronchi**, each leading into a lung, which is a richly vascularised sac, deeply and profusely pitted internally, thereby increasing the surface-area. The larynx itself is supported by a **cricoid** and a pair of **arytenoid** cartilages. The breathing (ventilation) movements of the frog are described on page 425.

Nervous System

The general classification of the component parts of this system is the same as for the dogfish, to be found on page 97. As in the case of that animal, they will be treated individually .

(A) BRAIN. Like that of the other Chordata the brain of the frog is primarily divisible into three regions. These are the fore-brain, mid-brain and hind-brain. The fore- and hind-brains are themselves each further subdivided into two parts, so that in all the brain consists of five regions. These, from in front backwards, are known as the telencephalon, the diencephalon, the mesencephalon (mid-brain), the metencephalon and myelencephalon. At the extreme anterior end of the **telencephalon** is a pair of small olfactory lobes, concerned with the sense of smell. The remainder of the telencephalon consists of a pair of comparatively large, elongated cerebral hemispheres, responsible for such phenomena as consciousness, memory and association (see Chapter 26). The cerebral hemispheres are thickened ventro-laterally, forming the **corpus striatum**, whilst the remainder of them constitutes the **pallium**. Behind them is a median **diencephalon**, known also as the thalamencephalon. The sides of this region are thick, and are known as optic thalami. From the roof projects the pineal stalk, representing the vestigial remains of a third eye in ancestral forms. The floor is produced downwards to form the

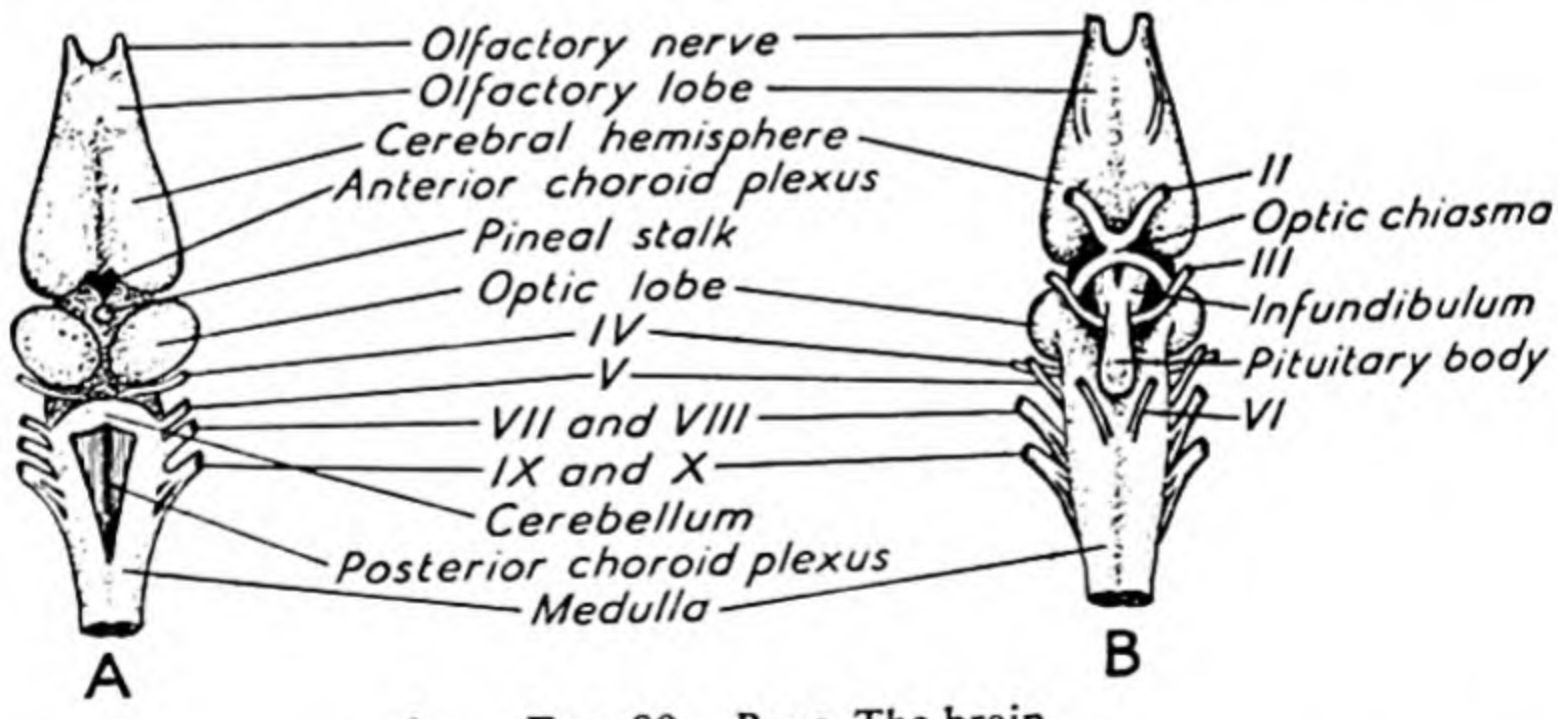


FIG. 90 – *Rana*. The brain.
A., Dorsal view; *B*., Ventral view.

infundibulum, which becomes closely associated with an up-growth from the roof of the mouth, known as the hypophysis, to form the pituitary body.

The floor of the mid-brain, or **mesencephalon**, is formed of two longitudinal columns of nerve-fibres, known as the crura cerebri, whereas dorsally this region has become considerably thickened and expanded to form the optic lobes. From each optic lobe there passes ventrally an optic nerve. These run forwards, and cross beneath the floor of the posterior end of the telencephalon to form there the optic chiasma. Thus each eye is innervated from the optic lobe of the opposite side.

The **metencephalon**, or cerebellum, is a transverse band of nervous tissue, situated just behind the optic lobes. It functions to co-ordinate muscular movements. The **myelencephalon**, or medulla, receives nerves from the greater part of the head, including the ears, as well as a direct supply from the viscera. At its posterior end it passes insensibly into the spinal cord.

The brain itself is hollow, containing in its cavity, as does the spinal cord, cerebro-spinal fluid. The cavities of the fore- and hind-brains are known respectively as the **third** and **fourth ventricles**, connected by the **aqueduct of Sylvius** in the mid-brain, this cavity being extended laterally into each optic lobe. The cavity of the fore-brain is further subdivided, for the cavities of the cerebral hemispheres come to be known as the **first** and **second lateral ventricles**, each communicating with the third ventricle of the diencephalon by a **foramen of Monro**.

The brain is invested in two membranes. The inner one is known as the **pia mater**, and is delicate. It becomes very much infolded into the thin-walled roofs of the diencephalon and myelencephalon and is there highly vascularised, forming respectively the anterior and posterior **choroid plexus**. Enveloping the pia mater is a toughter, protective **dura mater**.

(B) SPINAL CORD. The spinal cord is a hollow tube contained within the cavity of the vertebral column, including the urostyle. Immediately surrounding the cavity of the cord itself is a collection of nerve-cells, constituting the grey matter. This grey matter becomes extended towards the surface in the form of two dorsal and two ventral horns. Enveloping the grey matter except at these horns is a cylinder of nerve-fibres, constituting the white matter. The significance of this arrangement of nervous tissue will be understood when the paths taken by nervous messages have been discussed in Chapter 26. The whole nerve-cord is enclosed in a pia mater and becomes quite deeply grooved along the mid-dorsal and mid-ventral lines to form the **dorsal** and **ventral fissures**.

(C) CRANIAL NERVES. Issuing from the brain are ten pairs of cranial nerves, passing from the cranium through various foramina to supply organs of the head, and, in the case of the last two pairs, to run to the viscera. Differences in distribution from those of the dogfish may well be associated with the loss of gills and most of the neuromast system. The first pair (No. I) are the **olfactory** nerves. These are not really nerves in the true sense, for they are formed from cells lining the nasal cavity,

processes from these cells having become extended backwards to penetrate the olfactory lobes. Similarly cranial nerves No. II, the **optic** nerves, are merely extensions outwards of the brain itself, and are not true nerves. Nerve No. III on each side is known as the **oculo-motor,** and, together with Nos. IV and VI, innervates the eye-muscles. The disposition of these latter is precisely the same as those of the dogfish, described on page 101. Each oculo-motor nerve supplies all the eye-muscles of its own side except the external rectus and the superior oblique. These are supplied respectively by nerves VI (**abducens**) and IV (**trochlear**). Nerve V is large and is known as the **trigeminal**, on account of its subsequent division into three branches. Just before it emerges from the skull it bears a swelling, known as a Gasserian ganglion. Immediately beyond this it divides into two branches, a superficial ophthalmic to the skin of the fore part of the head, and a second branch which, running posteriorly across the orbit, divides into a mandibular branch to the lower jaw and a maxillary to the upper. Cranial Nerve No. VII is the **facial**, arising laterally from the myelencephalon just behind the fifth. It penetrates the Gasserian ganglion, with which its own geniculate ganglion becomes coalesced, though the two are separate in the tadpole. On emerging from this ganglion it divides into a palatine branch to the roof of the mouth, and a hyomandibular branch. This latter becomes further subdivided into a hyoid branch to the hyoid apparatus and a mandibular branch to the lower jaw. Nerve No. VIII is the **auditory**, and is to be regarded as a specialised branch of the facial, with which it therefore arises. It runs into the auditory capsule of its own side to supply the functional part of the ear. Cranial nerve No. IX is the **glossopharyngeal** and quickly joins No. X, passing through the ganglion of the latter. It then separates from it again almost immediately to become expanded into a petrosal ganglion of its own, after which it runs forwards to supply the floor of the mouth and associated structures. Nerve No. X, the **vagus**, is the largest of them all and arises by several roots from the posterior end of the myelencephalon. It bears a large vagus ganglion, and is concerned with the innervation of the viscera, supplying branches to the larynx, lungs, heart and stomach. On page 102 will be found a table indicating the disposition of the cranial nerves of the dogfish, from which that of the frog differs but little except in respect of nerve VII and the supply to the gill-slits of *Scyliorhinus*.

(D) SPINAL NERVES. There are ten pairs of spinal nerves, emerging on each side through the foramen enclosed between every two successive vertebrae. The last pair arises from two such apertures a short distance behind the front end of the urostyle. It will be observed in dissection that the region of emergence of each nerve is marked by the deposition of a soft, white, calcareous concretion. Each spinal nerve arises by two roots, arranged one above the other. The upper one is known as the **dorsal root**, and before leaving the vertebral column, which it does

in common with the lower **ventral root**, it bears a swelling, termed a **dorsal root ganglion**. Once outside the vertebral column the two roots join, only to divide again almost at once into a short **ramus dorsalis** and a much longer **ramus ventralis**. The former is concerned with the transmission of impulses from the skin into the grey matter of the spinal cord. The ramus ventralis, on the other hand, carries impulses outwards from the grey matter to the muscles of its own segment. From the ramus ventralis arises another short branch, known as the **ramus communicans**, which connects each spinal nerve with an autonomic nerve cord, running along each side of the dorsal aorta and later to be described (see below). The first spinal nerve of the frog is known as the **hypoglossal** and arises behind the first vertebra to supply the muscles of the tongue. What should really be the first – *i.e.* a nerve arising in front of the first vertebra – is represented only in the embryo and quickly disappears. The second spinal nerve is very stout and receives branches from both the first and the third, forming the **brachial plexus**, before continuing as the **brachial nerve** into the arm, The portion of the third spinal nerve beyond the brachial plexus and the whole of the fourth, fifth and sixth nerves proceed outwards to supply the skin and muscles of the posterior part of the trunk. The seventh, eighth, ninth and tenth spinal nerves unite to form a **sciatic plexus**, from which emerges a series of nerves to pass into the leg, the main trunk forming the **sciatic nerve**. The tenth nerve is very slender and emerges through a small foramen in the urostyle.

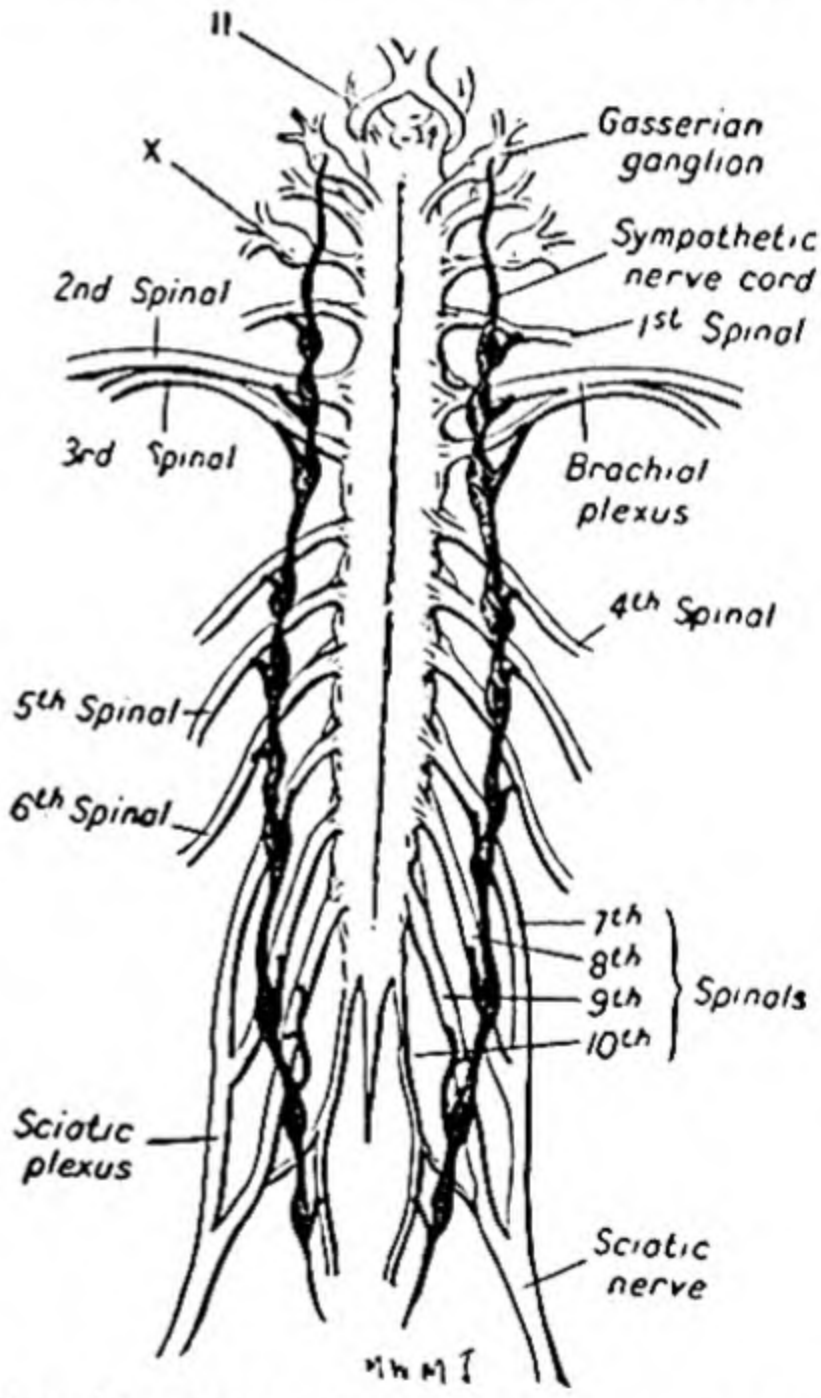


FIG. 91 – *Rana*. Spinal nerves; somewhat diagrammatic.

(E) AUTONOMIC NERVOUS SYSTEM. This consists essentially of a slender cord, running on each side of the dorsal aorta posteriorly, and diverging in front to accompany each systemic arch. As already pointed out, it is joined by a ramus communicans to each spinal nerve, each junction being marked by an **autonomic ganglion**. The cords themselves are double between the first two ganglia, and through each loop thus formed runs a subclavian artery. Anteriorly

each autonomic nerve-cord enters the skull, and establishes a connexion with the tenth nerve before running into the Gasserian ganglion of its own side. The autonomic nerve-cords are joined at intervals by branches, and are concerned with the innervation of the blood-vessels and viscera. The general structure of the autonomic nervous system, with special reference to the mammals, is described on page 466.

Sense Organs

There are three paired sense organs in the frog, namely the nasal organs, the eyes and the ears.

(A) NASAL ORGANS. These are situated one in each nasal capsule, and communicate with the exterior by the nostrils and with the mouth by the internal nares. The lining of each chamber is somewhat folded and is in connexion by the olfactory nerves with the pair of olfactory lobes. Stimulation is brought about by direct contact of particles of odoriferous substances with the endothelium.

(B) EYES. The structure of the eye of the frog is essentially similar to that of the mammal, described in detail on pages 166–70. Reference to the eye-lids of the frog was made on page 110.

(C) EAR. The ear is in principle the same as that of *Scyliorhinus*, but it has no direct communication with the exterior. Each ear lies in an auditory capsule, in which it is supported by a liquid, known as **peri-**

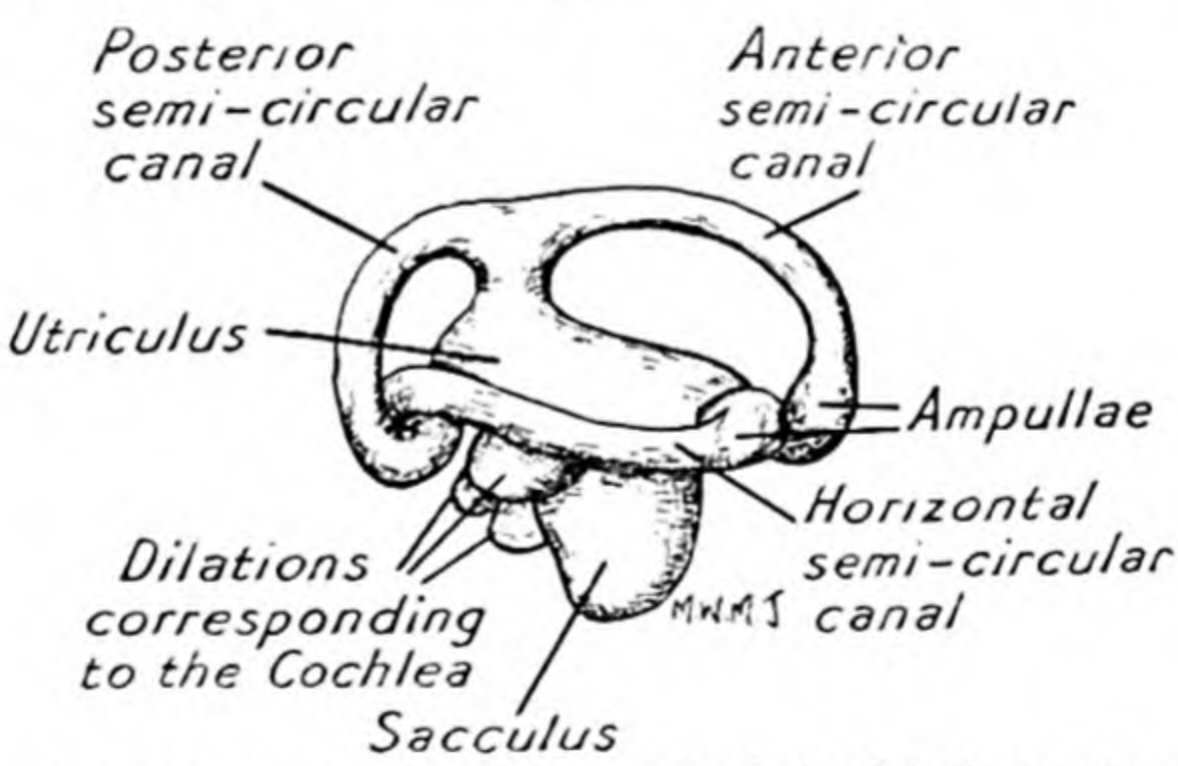


FIG. 92 – *Rana*. Membranous labyrinth of the inner ear.

lymph. It is essentially a hollow sac, very much evaginated and containing a fluid known as **endolymph**. It consists of a large **utriculus**, extended ventrally to form a somewhat smaller **sacculus**. From the utriculus there arise three semi-circular canals, an anterior and a posterior vertical at right angles to each other, and a horizontal canal, all opening into the utriculus at both ends, and each expanded at one end to form an **ampulla**. In the angle between the sacculus and utriculus lie three short evagina-tions, representing the **cochlea** of higher forms. The auditory capsule

itself is closed off from the cavity of the Eustachian tube by a membrane stretched across the fenestra ovalis, whilst this membrane is connected with the tympanum on the surface of the head by the columella auris. Thus vibrations are conveyed first to the tympanum, and then through the columella to the membrane over the fenestra ovalis. This sets up vibrations in the perilymph, and these are in turn transferred to the endolymph. Consequently impressions are conveyed to the myelencephalon via the auditory nerve. Only the sacculus apparently serves any auditory purpose, the semi-circular canals functioning to maintain equilibrium. An extension of the original ductus endolymphaticus passes down the neural canal to make contact with the calcareous masses on either side of the vertebral column: their function is unknown.

Urino-genital System

The functions of excretion (elimination of waste products in solution) and elaboration and evacuation of genital products are largely accommodated by the same organs, so that the organs concerned are classified into one composite system. Though the actual excretory organs are similar in both sexes it will be found convenient to describe the two sexes separately, including both reproductive and excretory organs. It must be first observed, however, that when blood passes through the liver its nitrogenous waste matter is mostly converted into urea. When this blood subsequently reaches the kidneys the urea is extracted, ready for elimination. In both sexes the kidneys are a pair of elongated, oval bodies, reddish in colour, lying dorsally in the posterior part of the abdominal cavity.

(A) MALE. Spermatozoa are produced in the testes. These are a pair of small, rounded, white structures, situated one laterally to the anterior end of each kidney. The spermatozoa are conveyed from each testis by a system of fine tubules, known as **vasa efferentia**, to the kidney of the same side. From here both sperms and urine take the same path to the exterior. They pass first along a short Wolffian duct, which opens from the posterior end of the kidney and which bears a lateral diverticulum, known as the vesicula seminalis, where sperms are stored. The Wolffian duct of each side opens into the dorsal side of the rectum, whilst ventral to the rectum arises a median urinary bladder, which becomes expanded to form a bi-lobed structure where urine is stored, being shed to the exterior at intervals through the cloaca.

(B) FEMALE. Eggs are produced in a pair of large ovaries, formed by a folding process from the coelomic epithelium (peritoneum). When ripe the eggs are shed into the body-cavity, from which their only means of escape is through a pair of funnels, situated one on either side of the oesophagus. These lead into long, coiled tubes, known as oviducts or Müllerian ducts, which open into the cloaca just before this latter receives the Wolffian ducts from the kidneys, which are arranged as in

the male. At its base each oviduct becomes expanded to form an egg-sac, where eggs may be stored. A bladder occurs, similar in structure and position to that of the male. The oviducts themselves secrete a slimy

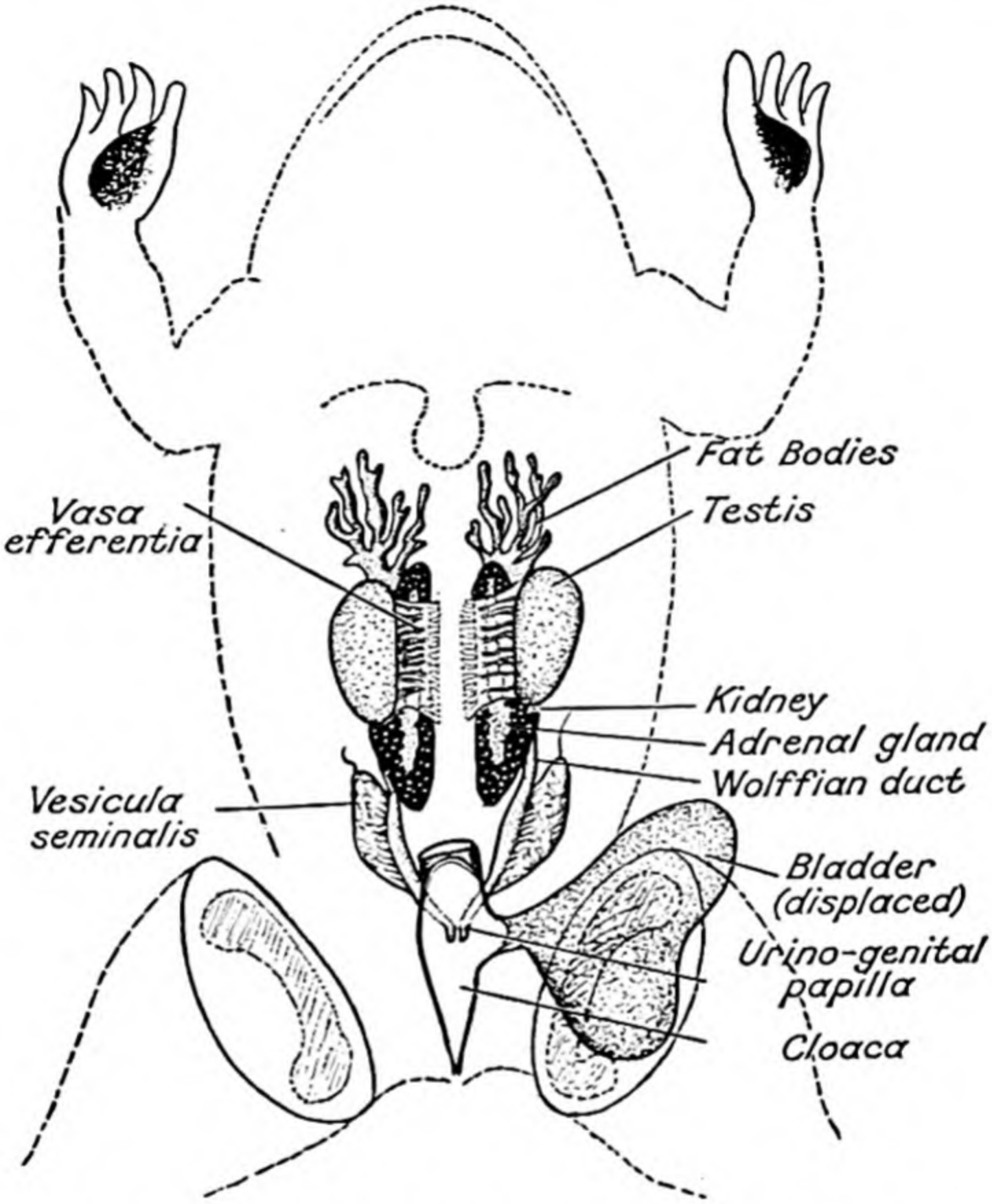


FIG. 93 – *Rana*. Dissection of male urino-genital system.

substance around the eggs, and this expands and hardens to form the characteristic jelly when coming into contact with water.

(C) REPRODUCTION. The breeding season is in March, and pairing occurs. The male climbs on to the back of the female and clasps her with his fore-limbs, maintaining his grip by means of the roughened thumb-pads, which are especially well developed at this season. In this position the frogs may remain for days, until the female finally lays her eggs. When this occurs the male sheds sperm over them, so that there is a

reasonably good chance of every egg becoming fertilised. Once mating is completed, the female croaks to deter any male attempting to mount her. Thus, unlike the condition in the dogfish but resembling that of

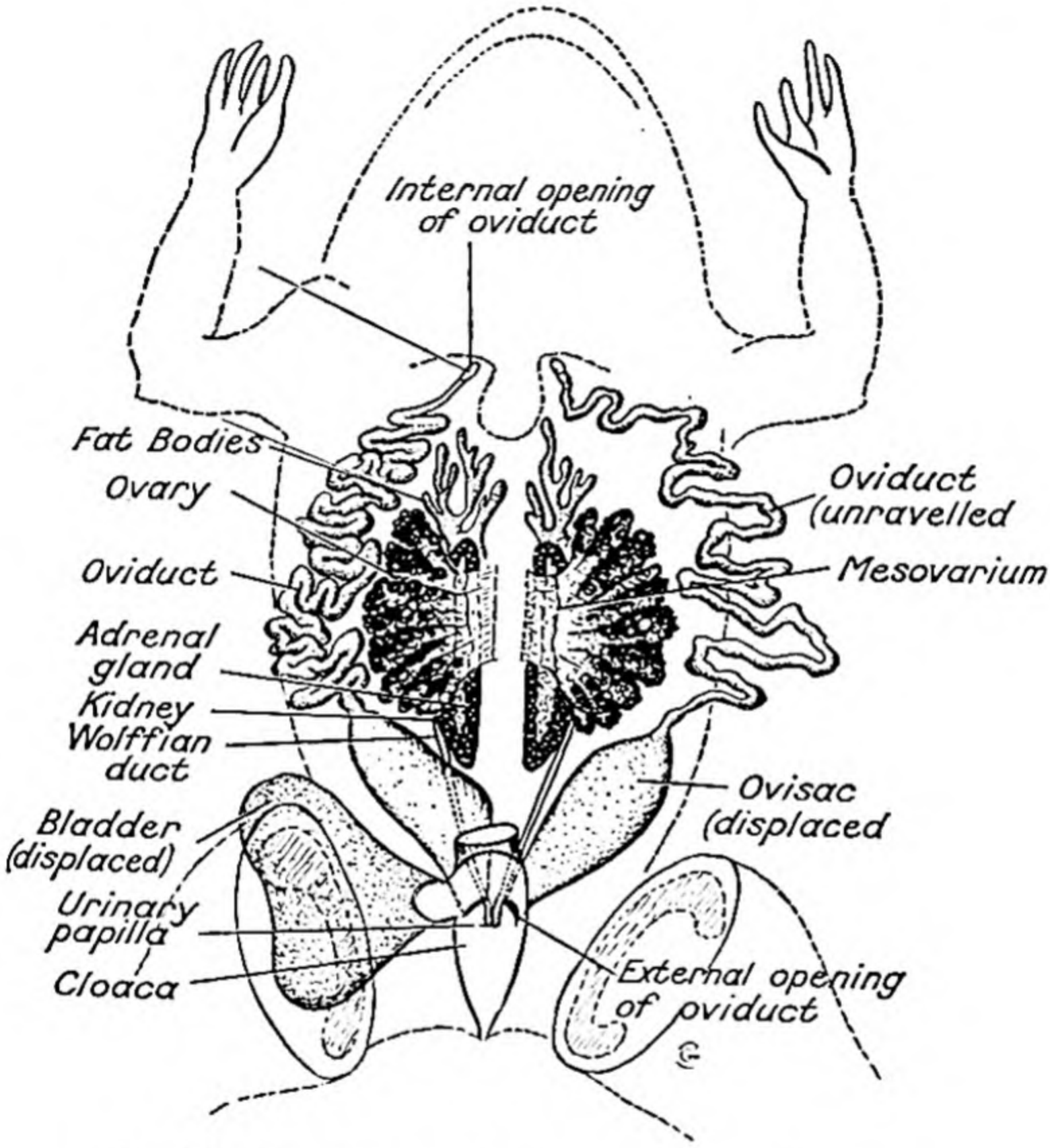


FIG. 94 – *Rana*. Dissection of female urino-genital system.

most other fish, fertilisation is external, and once the spawn is deposited the parents take no further care of it.

Endocrine Organs

The significance of the substances produced by these glands and poured into the blood-stream is considered in Chapter 27. Here it is necessary to discover the structure and position in the body of the glands themselves.

The **thyroid gland** is in the form of a pair of small, rounded lobes on the external jugular veins, not far removed from the heart.

The **thymus** is a small, oval gland, lying on either side of the head, just within and behind the tympanum.

The **pituitary body**, consisting of hypophysis and infundibulum (page 480), lies ventral to the diencephalon.

There is an **adrenal body** situated in the ventral face of either kidney. It is essentially of double origin, consisting of a **medulla**, of nervous origin, and a **cortex**, derived from the coelomic epithelium, though these components are indistinguishable in the frog's adrenal bodies. In lower forms these two components remain separate as the supra-renal and inter-renal bodies respectively, as already noted in *Scyliorhinus*. When they become fused the adrenal bodies are at first not compact, but occur in strips along the autonomic nerve-cords. This condition is represented in the newt. The pair of **carotid glands** in the frog, situated at the junction of the internal and external carotid arteries, affords the last remains of these strips.

PRACTICAL WORK

This animal must be dealt with very thoroughly, since it demonstrates all the features of vertebrate anatomy, though in a somewhat specialised condition, and is quite easily obtained. During the course it should be dissected at least three times. On the first occasion dissect the alimentary system first, but subsequently start with the vascular system, so that this may be dissected while the specimen is still fresh, and hence the blood-vessels still conspicuous. The skeleton should be studied and drawn in detail.

CHAPTER 8

Oryctolagus

The common rabbit, *Oryctolagus cuniculus*, is well known both in the wild and domesticated condition. It was introduced into Britain by man from Mediterranean countries, and following its subsequent carriage to Australia it found climatic conditions so suitable in that country that it has become a pest. It lives in burrows, and these are arranged in small communities. It is crepuscular in its habit, this to some extent being a protective adaptation, for the animal is herbivorous and has practically no means of defence against its carnivorous enemies. The rabbit is a member of the class Mammalia. Members of this class are characterised by certain diagnostic features. They are warm-blooded, this signifying that the temperature of their blood remains more or less constant. This property they share, of course, with birds. The body is invested in a partial or complete covering of hair, this assisting in the conservation of body-temperature by preventing the loss of heat to the exterior. The young are born alive and are suckled – *i.e.*, they are fed on a milk secreted by the mammary glands of the mother.

External Characters

The covering of hair to the body of a rabbit is almost complete. At the posterior end the vertebral column becomes extended backwards to form a true tail, invested in skin and fur. The under surface of the tail is white in colour, and this is suggested as being of protective significance to other members of the community, for, on approach of danger, one individual may the more easily be seen by others to be moving towards its burrow, when the remainder tend to behave similarly. The body is clearly divisible into head, neck, trunk and limbs. Beneath the tail is the **anus**, through which faeces are shed to the exterior. Ventral to this lies the urino-genital aperture, borne in the male on a **penis** and known in the female as a **vulva**. In the adult male there may be seen, on either side of the penis, a **scrotal sac**, containing a testis. This is a feature characteristic of adult males of most mammals. On the head the most conspicuous feature is a pair of long external ears, or **pinnae**, functioning for the collection of sounds. Each eye has an upper and lower lid, and the transverse eye-lid of the frog is represented in many mammals by a small **nictitating membrane** in the inner corner of each eye. In the rabbit it remains functional, being used to clean the conjunctiva. The upper lip is deeply cleft in the centre and is known as a **hare-lip**. On either side of the snout is a number of

long, sensitive whiskers, known as **vibrissae.** Along the ventral surface of the trunk of the female lie some four pairs of **nipples,** which contain the apertures of the mammary glands. In both sexes a pair of pits, one on either side of the anus, mark the openings of the pair of **perineal glands,** to whose secretion the characteristic smell of the rabbit is due. The limbs are built on the same plan as in the frog and each digit terminates in a hard claw.

Skin

The skin is clearly divisible into an ectodermal epidermis on the surface, and a mesodermal dermis within. The former is further sub-

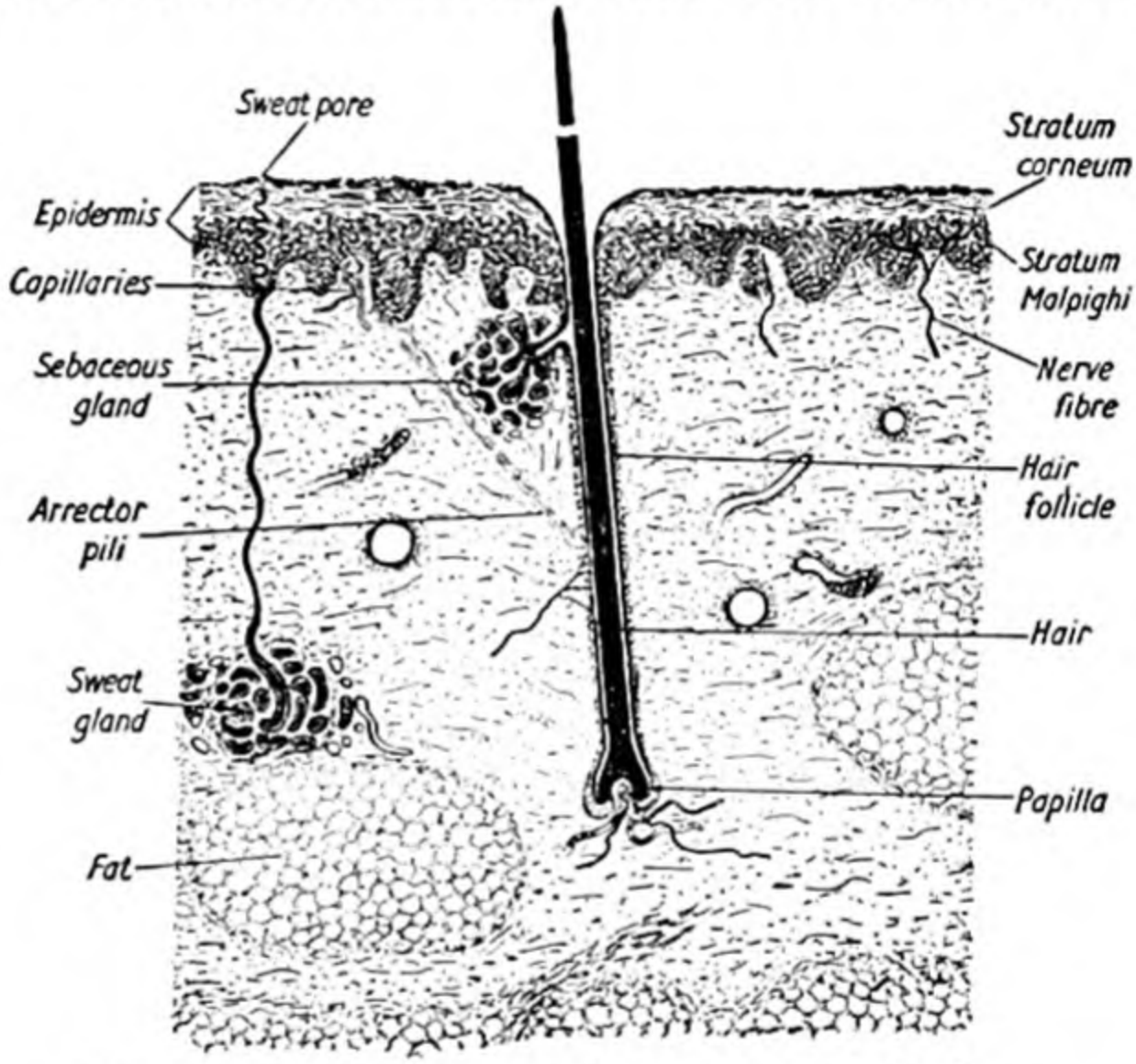


FIG. 95 – Vertical section of the skin of mammal.

divided into a superficial **stratum corneum** and an underlying **stratum Malpighi.** This latter is composed of actively-dividing cells, the products of this division passing outwards to form the flattened horny scales of the stratum corneum. Separating the stratum Malpighi from the stratum corneum are the **strata granulosum** and **lucidum,** composed of cells showing degenerative changes as their death occurs and they become horny. The dermis itself is mainly connective tissue, and contains considerable quantities of fat. Running in the dermis are blood-vessels and nerves, the latter acquiring a connexion with sensitive cells of the epidermis. At intervals the innermost layer of the stratum Malpighi becomes invaginated to form a pit in the dermis. This is a **hair-follicle,** cells at the base of which multiply to bring about the growth of the hair. Each hair itself is divisible into a central medulla, surrounded by a pigmented cortex and

covered by a thin cuticle. The cells composing the hair are, like the surface cells of the epidermis, dead and cornified, and are elongated in the direction of the (keratinised) axis of the hair. Beneath the dermis occur muscles concerned in the movements of the skin. As well as the structures already described there are three kinds of glands found in the skin, all of epidermal origin. The **sweat glands** are sunk deep into the dermis, where each ends in the form of a much-coiled, blind tube. They are important in the regulation of body-temperature, for they acquire water from neighbouring blood-vessels, and this is cast on to the surface. Here evaporation occurs, and the latent heat required to effect this process is obtained from the animal, which thus becomes cooled. **Sebaceous glands** are concerned with the production of the greasy substance associated with the hairs of the rabbit. Their secretion is actually liberated by the complete destructions of the cells, new ones being formed from the base, itself derived from the stratum Malpighi. The glands open into the hair-follicles. The perineal glands belong to this class, as also do the **Meibomian glands** along the edges of the eye-lids. The secretion of these latter serves to clean the cornea of particles of dust when the rabbit closes and re-opens its eyes. They are assisted in this function by the watery secretion of the **lachrymal glands**, situated one in the inner corner of each eye. Surplus secretion drains away into the nasal cavity. The **mammary glands** occur in both sexes, but become functional only in the female. Each is a branched tube lying between the dermis and the muscles beneath: it is, in fact, a highly-specialised sebaceous gland. Mammary glands open on to the surface by the nipples. A somewhat remarkable adaptation in Mammalia in general is the approximate correspondence of the number of nipples to that of young born in a litter.

Skeleton

It is assumed here that the reader will at this stage have already studied the skeleton of the frog, so that certain points concerned with general structure of the skeleton will now be omitted. The skeleton of the rabbit is almost entirely bony, but it is represented first by cartilage, which subsequently becomes replaced by cartilage-bone, whilst membrane-bones contribute a good deal to the skeletal architecture. Each portion of the skeleton will be described in turn, but, owing to its greater suitability for practical work, the skull of the dog will be substituted for that of the rabbit, though the two are in most respects essentially similar.

(A) VERTEBRAL COLUMN. Like that of the frog, the vertebral column is made up of a number of vertebrae, articulating end to end to form a hollow tube. Each vertebra consists of a centrum composed, in the young animal, of two terminal plates of bone, known as **epiphyses**. Between each epiphysis and the remainder of the centrum is a certain amount of cartilage, thus allowing for growth. The exposed surfaces of the epiphyses are flat, unlike the condition in the frog (page 116), where

saddle joints occur between neighbouring vertebrae. Separating consecutive centra are pads of fibro-cartilage, known as **intervertebral discs**. These prevent friction and act as shock-absorbers. In the centre of each is very soft material, known as the *nucleus pulposus* and representing the embryonic notochord. From the centrum arise neural arches, joining above to enclose the nerve-cord. In the mid-dorsal line arises a neural spine, whilst transverse processes and articulating surfaces (zygapophyses) also occur. But whereas all the vertebrae of the frog are essentially the same, the vertebral column of the rabbit is clearly regionally differentiated, the vertebrae of the various portions being characterised by certain well-defined features.

(i) *Cervical region.* In all mammals except three species there are seven cervical vertebrae. To each of these there is fused on either side a short **cervical rib**, the tuberculum (page 143) of the rib articulating with the transverse process of the vertebra, and the capitulum (page 143) with the centrum. This fusion takes place in such a way as to enclose a foramen through which passes the vertebral artery; this foramen is known in consequence as the **vertebrarterial canal**. The first cervical vertebra is peculiarly modified, and is known as the **atlas**. It has no centrum, and in life its cavity is divided transversely by a ligament, the spinal cord passing through the upper chamber and the odontoid process of the second cervical vertebra projecting into the lower. Expanded processes, con-

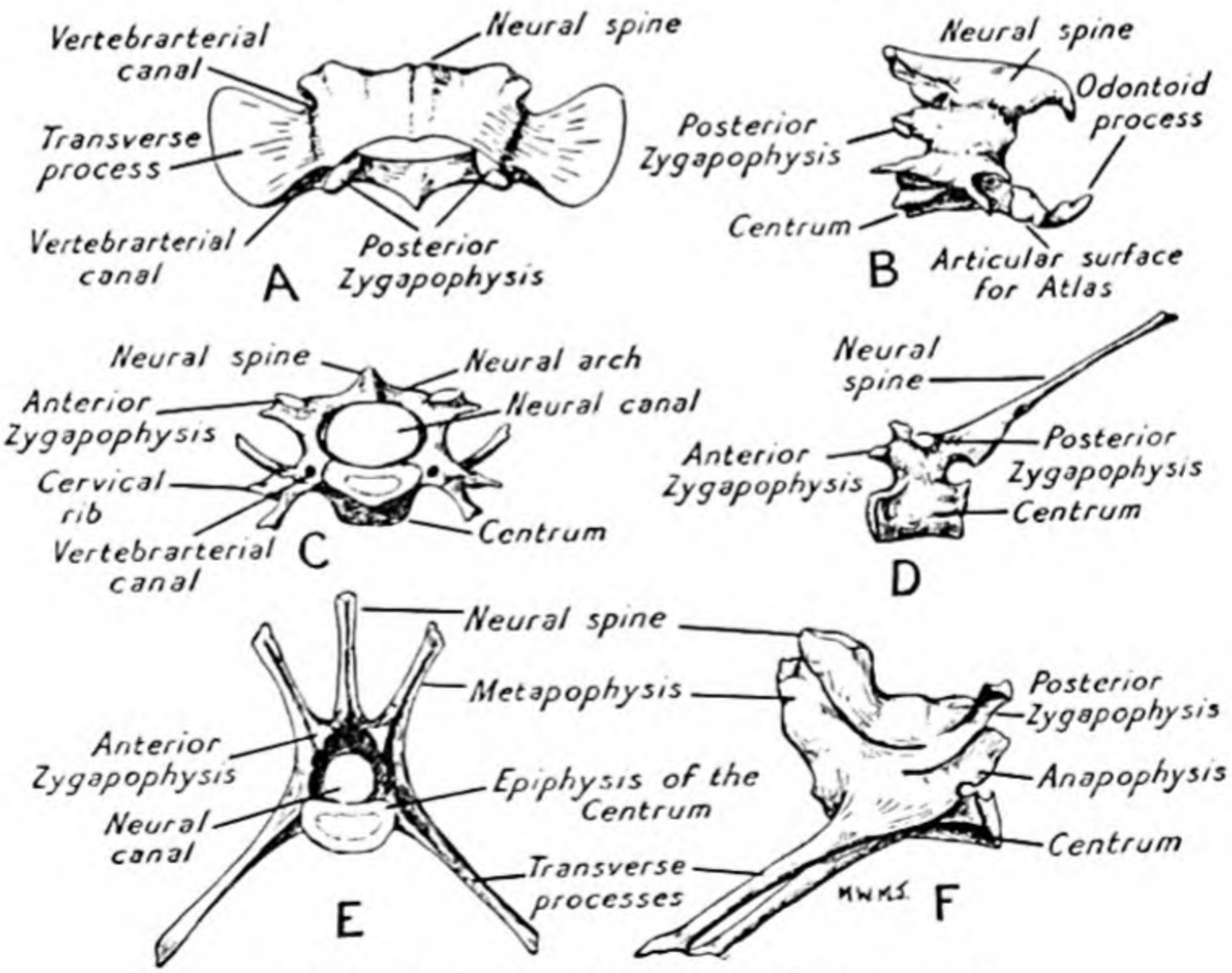


FIG. 96 – *Oryctolagus.* Representative vertebrae.
A., Atlas; *B.*, Axis; *C.*, Cervical; *D.*, Thoracic; *E.* and *F.*, Lumbar.

sisting of transverse processes and cervical ribs indistinguishably fused, function for the attachment of muscles moving the skull. The second cervical vertebra, known as the **axis**, is peculiar in that the anterior end of its centrum bears a blunt projection, known as the **odontoid process**. This is morphologically the centrum of the atlas, having become fused with that of the axis during development.

(ii) *Thoracic region.* There are usually twelve thoracic vertebrae, characterised by two facets on either side for articulation with the movable ribs.

(iii) *Lumbar region.* Seven is the usual number of lumbar vertebrae, which may be distinguished by their large transverse processes. In addition the zygapophyses are well developed. The anterior zygapophyses are borne each on the inner side of a large **metapophysis**, and the posterior end bears a pair of **anapophyses**, each overhanging the intervertebral notch of its own side.

(iv) *Sacral region.* This consists usually of one, but occasionally of two, vertebrae, and receives the ilia of the pelvic girdle, for which purpose expanded processes occur, formed by the fusion to the vertebra or vertebrae of sacral ribs. A number of vertebrae immediately behind this region are fused with the sacral vertebra(e), and the whole mass constitutes the **sacrum**.

(v) *Caudal region.* This is made up of some eighteen vertebrae. The first two or three are fused with the sacrum, and the hinder ones remain separate, becoming progressively more degenerate, until finally they are nothing more than minute rods of bone.

(B) RIBS AND STERNUM. There are twelve pairs of ribs forming a skeletal support for the wall of the thorax or chest. These ribs articulate dorsally with the thoracic vertebrae by a double facet, a **tuberculum** articulating with the transverse process of its vertebra and a **capitulum** with the centrum. The last three pairs of ribs have no tubercula. In the mid-ventral line is the breast-bone, or **sternum**. This is divided transversely into six **sternebrae**, the most anterior of which is attached to the clavicle, and to the posterior is attached a **xiphisternum**, bearing at its free end a plate of cartilage, known as the **xiphoid cartilage**. The first seven ribs articulate ventrally with the sternum, whilst the eighth and ninth are attached to the seventh, the attachment being effected by bands of cartilage to give flexibility. The last three end freely at their ventral extremities, and are known as floating ribs.

(C) PECTORAL GIRDLE AND FORE-LIMB. The pectoral girdle is somewhat degenerate when compared with that of lower forms. This may be accounted for by the development of ribs, which renders it no longer necessary for this girdle to be in the form of a hoop of bone to support this region of the body. The two halves have become completely independent, and each is composed almost entirely of one bone, the **scapula**, or shoulder-blade. This bears a ridge along its outer face. From

the glenoid end of the ridge (Fig. 97, *A*) arise two processes – the *acromion* and the *metacromion*, serving for the attachment of muscles. Overhanging the glenoid cavity is a short coracoid process, representing the coracoid of lower forms. Joining the acromion to the first sternebra is a slender clavicle, or collar-bone, whilst along the dorsal border of the scapula runs a narrow rod of cartilage, the suprascapula.

The bone of the upper arm is known as the **humerus**, the head of which fits into the glenoid cavity of the pectoral girdle of its own side. In front

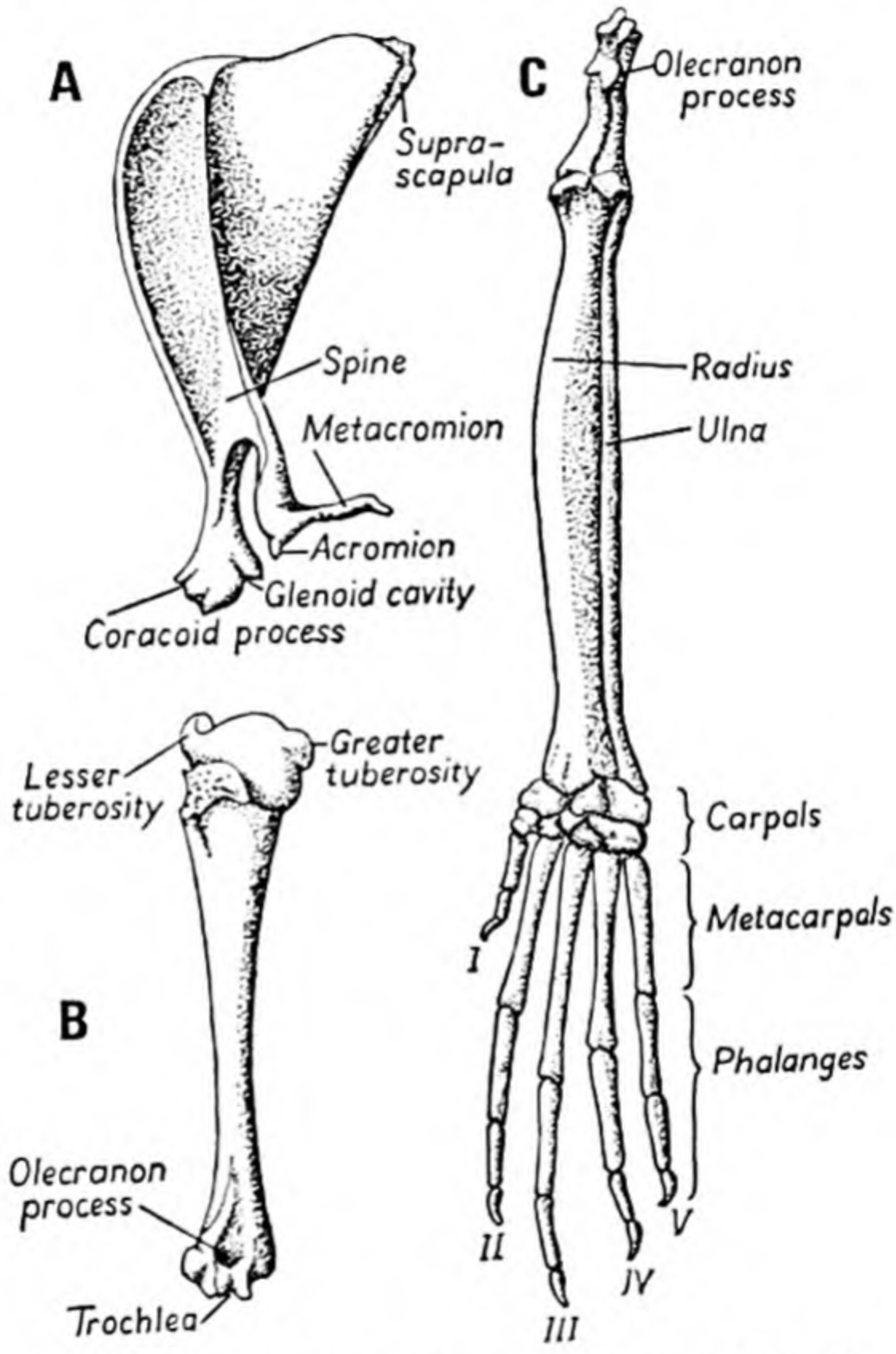


FIG. 97 – *Oryctolagus*. Pectoral girdle and forelimb.
A., Scapula; *B*., Right humerus in back view; *C*., Lower part of front leg in front view.

of the head of this bone lies the **bicipital groove**, bordered on the inside by the **lesser tuberosity**, and on the outside by the **greater tuberosity**. Running along the ventral side is a deltoid ridge. At the distal end is a groove, known as the trochlea, for the reception of the ulna. Just above

this, on the front of the bone, is a depression, known as the **coronoid fossa**, whilst in a corresponding position on the under surface is an **olecranon fossa** for the reception of a projection of the ulna when the arm is straightened out. The two fossae are in communication by a **supratrochlear foramen**, pierced in the part of this bone which has become thin owing to the formation of these fossae. The fore-arm is made up of two separate bones, the **radius** and the **ulna**. In the rabbit these are fixed, but in man the lower end of the radius may be orientated to a limited extent about the ulna. Thus the two bones may lie parallel to each other, as when the arm is stretched forwards with the palm pointing upwards. This position is known as that of **supination**. When the palm is turned downwards rotation of the radius about the ulna occurs and the position is described as that of **pronation**. In *Oryctolagus* the bones are permanently fixed in the prone position. The wrist, or **carpus**, is composed of three proximal carpals, known as the radiale, intermedium and ulnare, whilst articulating with these are a central carpal and four distal ones, termed the trapezium, trapezoid, magnum and unciform. There are five **metacarpals** all bearing 3 **phalanges**, except the first, which has only 2.

(D) PELVIC GIRDLE AND HIND-LIMB. As in the frog the pelvic girdle consists of two identical halves, fused in the middle line, and each consisting of **ilium**, **ischium** and **pubis**. The two halves together form a hoop-like structure in the posterior part of the body-wall. Each ilium extends forwards and upwards to become attached to the sacrum. Behind the **acetabulum** – the depression into which fits the head of the femur – is the ischium. Also ventral and anterior to this lies the pubis. The three bones fuse together at the acetabulum. The ischium and pubis together enclose an **obturator foramen**, whilst the two pubes unite in the mid-ventral line to form a symphysis. The sacrum and two halves of the pelvic girdle together constitute the **pelvis**. Through the ring of bone thus formed pass both the gut and the urino-genital tract, so that in the female the embryo must also be passed through this ring prior to birth.

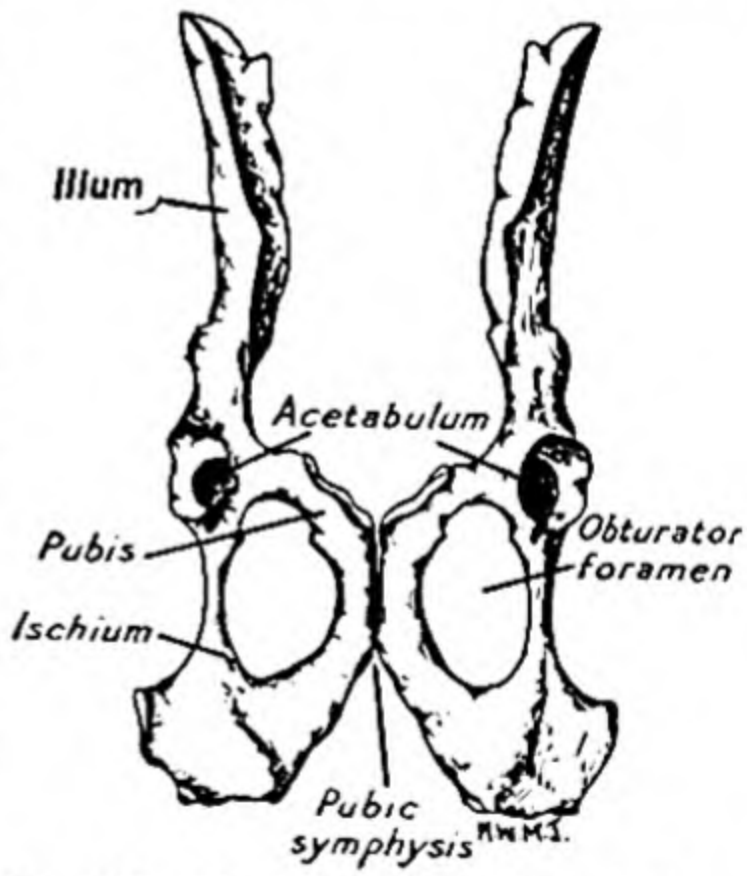


FIG. 98 – *Oryctolagus*. Pelvic girdle, in ventral view.

The bone of the thigh is the **femur**, the head of which fits into the acetabulum. Near the head and to the inner side is a **lesser trochanter**, whilst on the outer side of the head lies a **greater trochanter**. Both

trochanters serve for the attachment of muscles, whilst below there occurs a **third trochanter**. At the distal end of this bone are two condyles for the reception of the tibia. The shin, or lower-leg region, is formed of a large **tibia** (pre-axial) and a slender **fibula** (postaxial), the two being fused together at their distal ends. The joint between the femur and the tibia is covered by a small bone, known as the **patella**, or knee-cap.

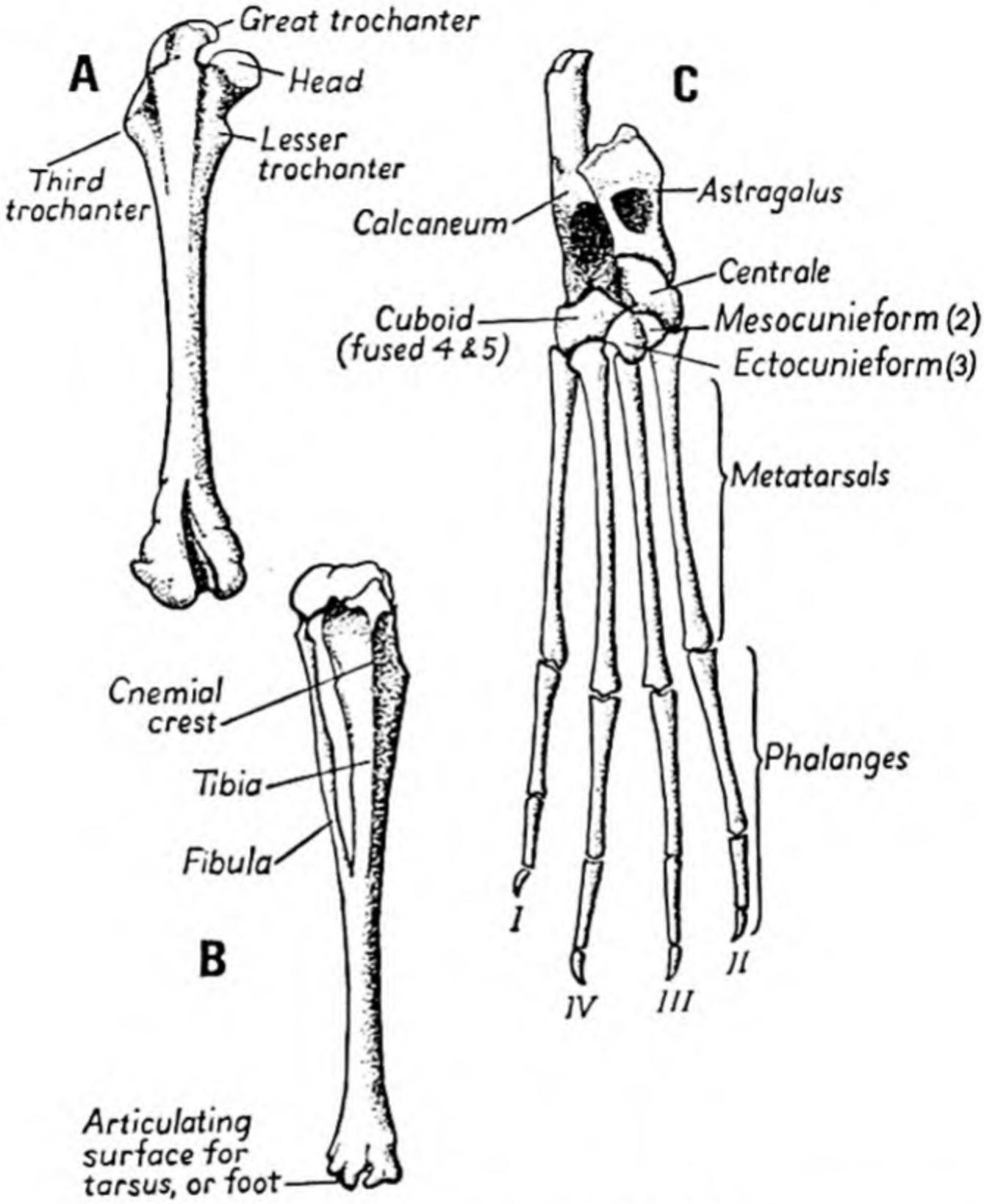


FIG. 99 – *Oryctolagus*. Hindlimb.
A., Right femur from in front; *B*., Right tibio-fibula from in front; *C*., The tarsus and foot.

Along the anterior surface of the tibia runs a prominent **cnemial crest**. The tarsus consists of two proximal **tarsals**, known as the astragalus (or tibiale) and calcaneum (or fibulare), whilst there is one central tarsal and three distal ones. These latter are in reality the 2nd (known as the meso-cuneiform, the 3rd (the ectocuneiform), and the fused 4th and 5th (the cuboid). There are only four **metatarsals**, each bearing 3 phalanges.

(E) SKULL. In the following description the skull of the dog will be taken as typical of that of mammals, and points of distinction from that of the rabbit will be mentioned. A knowledge of the skull of the frog will

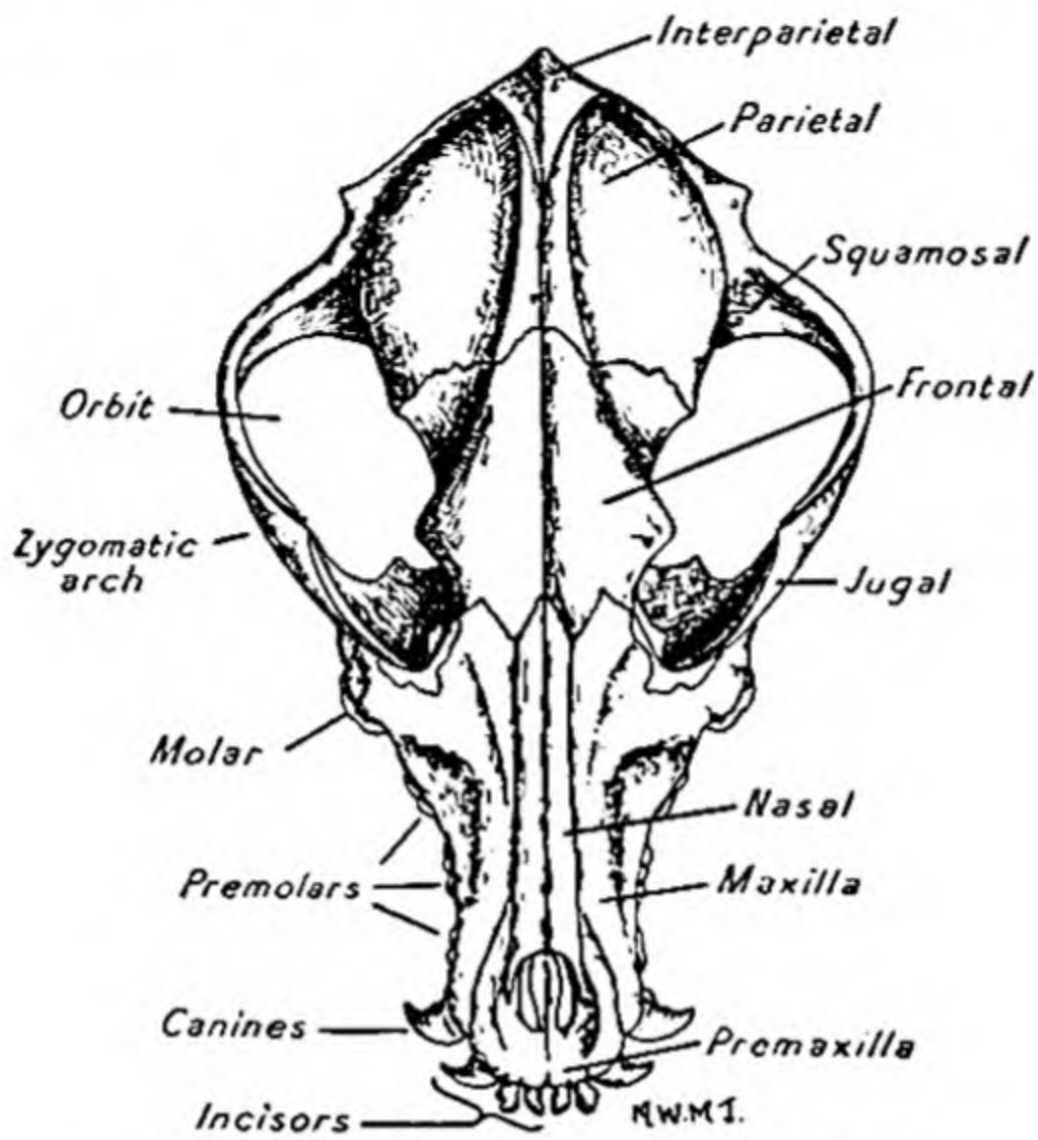


FIG. 100 – Skull of Dog. Dorsal view.

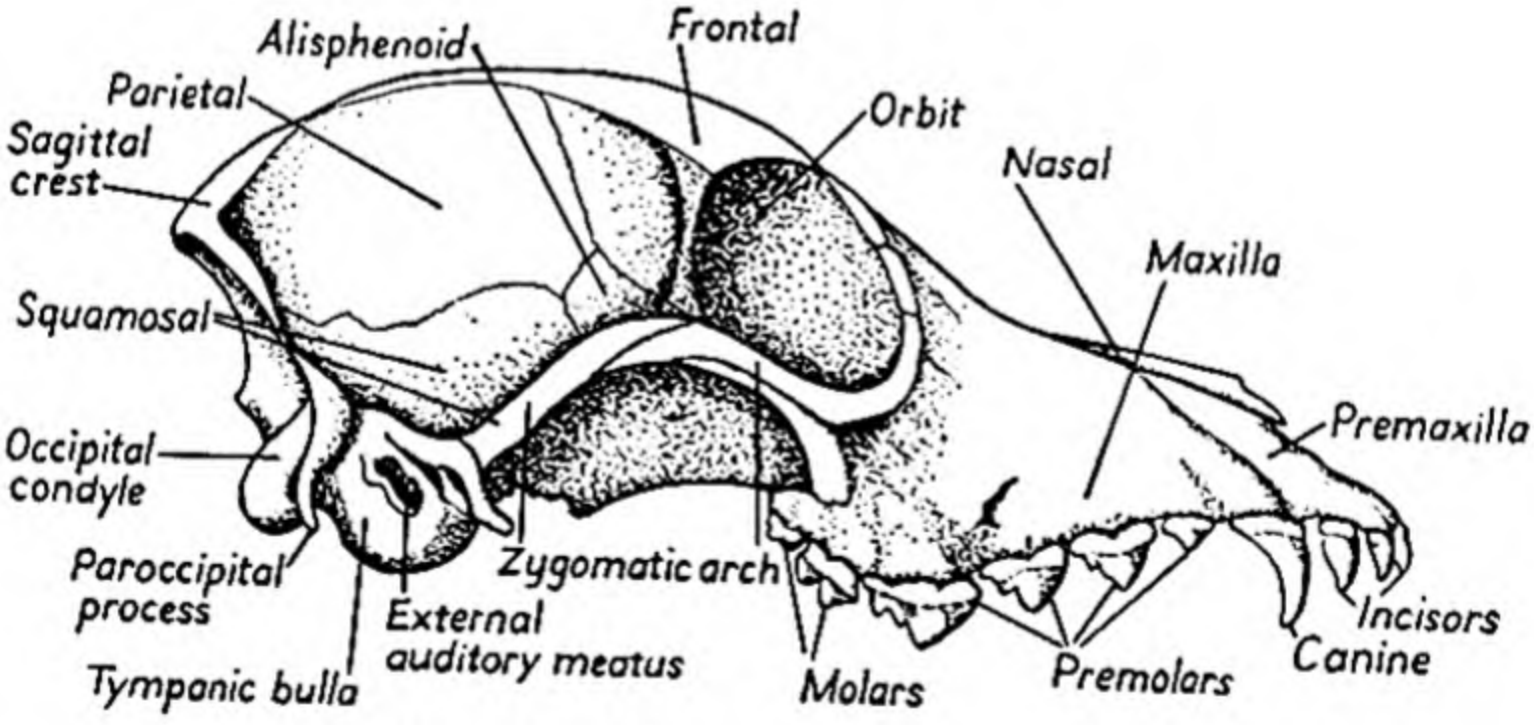


FIG. 101 – Skull of Dog. Lateral view.

be assumed. Considering first the cranium, the floor consists from the back end forwards, of **basioccipital, basisphenoid, presphenoid** and **vomer.** This is not homologous with the vomer of the frog, but represents the anterior end of the parasphenoid of the latter type. The roof consists of

a **supraoccipital** above the foramen magnum, and paired **parietals, frontals** and **nasals**. Each lateral wall of the cranium is made up of **squamosal, alisphenoid** and **orbitosphenoid**, whilst near the front end of the orbit occurs a small **lachrymal** bone. The **sphenethmoid** has become modified to form a **cribriform plate**, placed transversely so as to limit the forward extension of the cranial cavity. It is continued in front of this as

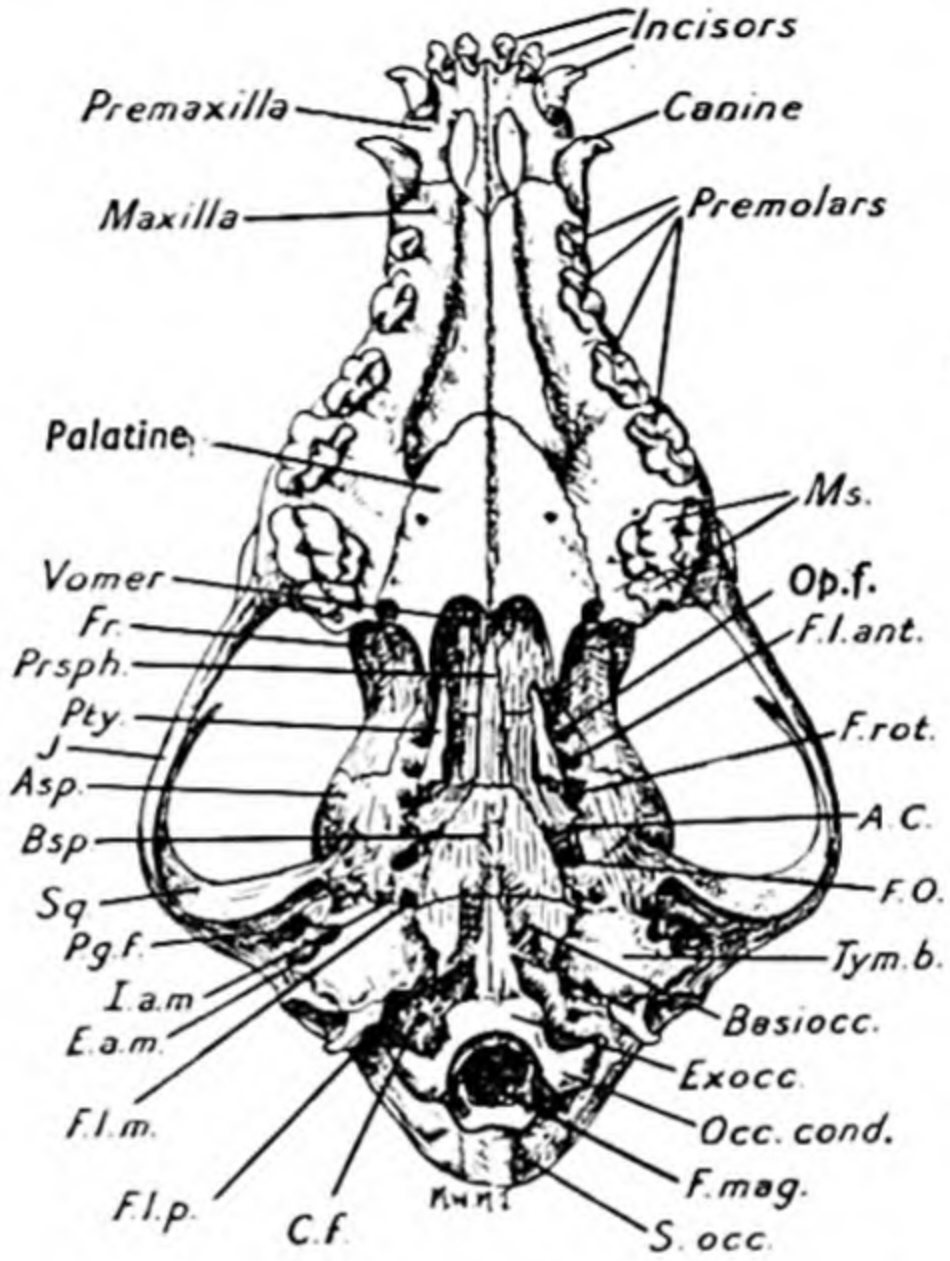


FIG. 102 – Skull of the Dog. Ventral view.
Asp., alisphenoid; *A.C.*, alisphenoid canal; *Basiocc.*, basioccipital; *Bsp.*, basisphenoid; *C.f.*, condylar foramen; *Exocc.*, exoccipital; *E.a.m.*, external auditory meatus; *F.I.ant.*, foramen lacerum anterius; *F.I.m.*, foramen lacerum medium; *F.I.p.*, foramen lacerum posterius; *F.mag.*, foramen magnum; *F.O.*, foramen ovale; *F.rot.*, foramen rotundum; *Fr.*, frontal; *I.a.m.*, internal auditory meatus; *J.*, jugal; *Ms.*, molars; *Occ.cond.*, occipital condyle; *Op.f.*, optic foramen; *P.g.f.*, post-glenoid foramen; *Prsph.*, presphenoid; *Pty.*, pterygoid; *Sq.*, squamosal; *S.occ.*, supra-occipital; *Tym.b.*, tympanic bulla.

a median, vertical plate of cartilage, separating the right and left nasal chambers. The cribriform plate itself is pierced by holes, through which pass branches of the olfactory nerves. Within the nasal cavities is a number of very thin **turbinal** bones, supporting the nasal endothelium. The auditory capsules are each bordered by a number of bones which have become fused to form the **periotic**. The tympanic cavity leading to the ear is enclosed in a flask-shaped membrane, the **tympanic bulla.**

Since the brain is thus enclosed within a cranium it is essential that **foramina** be present to permit the passage to and from the brain of nerves and blood-vessels. As the bones constituting the skull enlarge during development they meet each other, forming **sutures**. In many places a

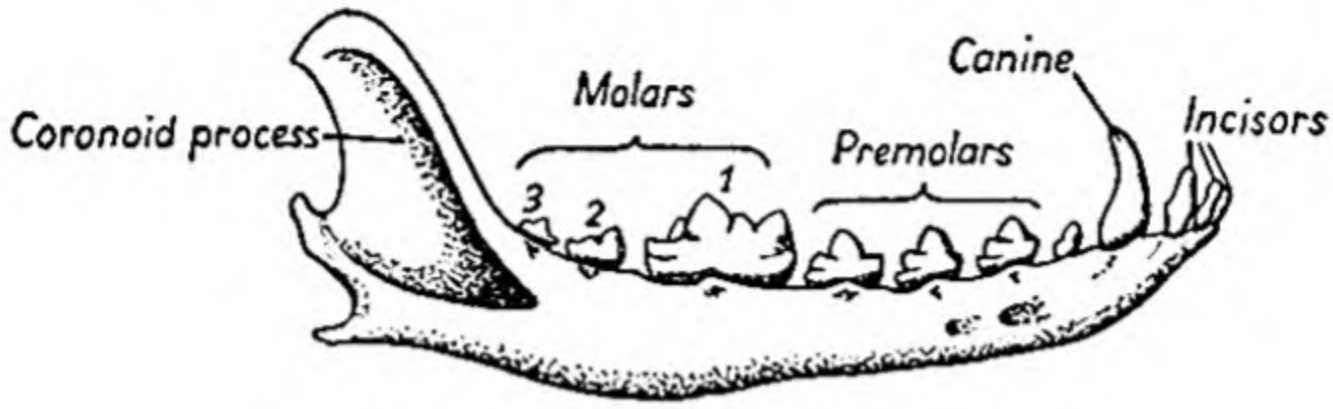


FIG. 103 – Skull of the Dog. Lower jaw.

foramen is formed by two bones failing to meet over a small area, but in other cases a bone may grow round a nerve or blood-vessel, present before the development of the bone, to form a foramen actually piercing the bone in question. Most of the important foramina occur in the orbit and posterior end of the skull. Starting posteriorly and working forwards, nerve XII passes through a **condylar foramen** in the exoccipital. Just in

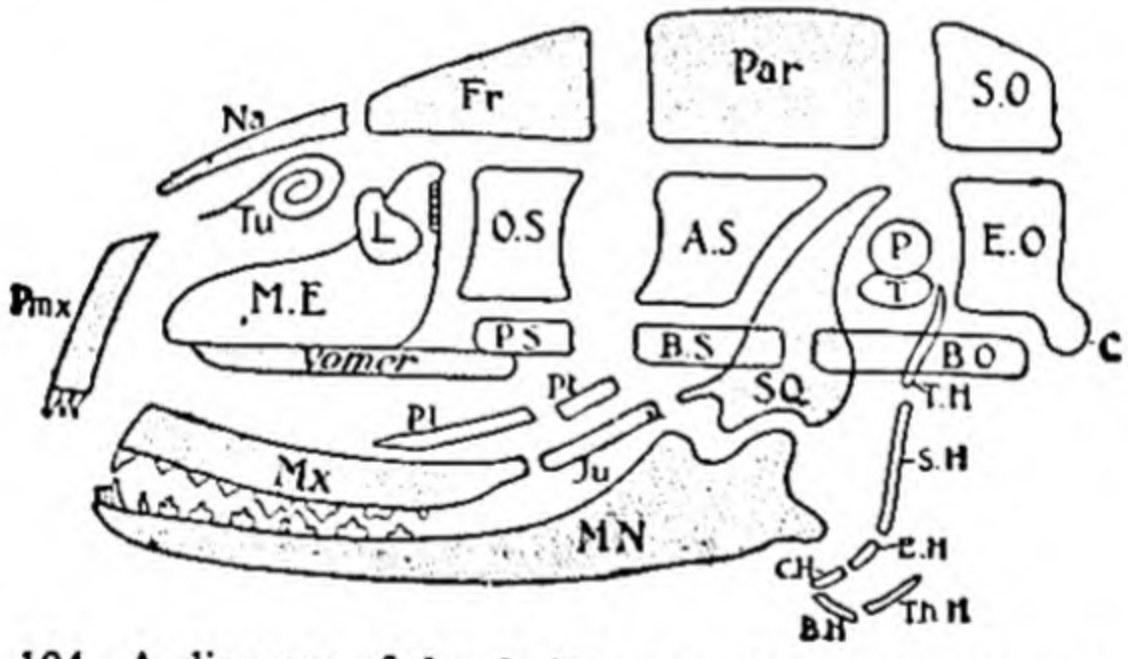


FIG. 104 – A diagram of the skull bones of a mammal (partly after Flower and Weber), with the membrane bones shaded. *B.O.*, Basioccipital; *E.O.*, Exoccipital; *C.*, Condyle; *S.O.*, Supra-occipital; *Par.*, Parietal; *Fr.*, Frontal; *Na.*, Nasal; *Pmx.*, Pre-maxilla; *M.E.*, Mesethmoid; *L.*, Lachrymal; *Tu.*, Turbinal; *P.S.*, Presphenoid; *O.S.*, Orbitosphenoid; *A.S.*, Alisphenoid; *B.S.*, Basisphenoid; *SQ.*, Squamosal; *P.*, Periotic; *T.*, Tym-panic; *Pl.*, Palatine; *Pt.*, Pterygoid; *Mx.*, Maxilla; *Ju.*, Jugal; *T.H.*, Tympanohyal; *S.H.*, Stylohyal; *E.H.*, Epihyal; *C.H.*, Ceratohyal; *B.H.*, Basihyal; *Th.H.*, Thyrohyal; *MN.*, Mandible. (From 'Manual of Zoology', by L. A. Borradaile. O.U.P.)

front of the exoccipital, between it and the periotic, is the **foramen lacerum posterius**, through which pass nerves IX, X and XI, together with the internal jugular vein. Between the tympanic bulla and the periotic is the **stylo-mastoid foramen** for nerve VII. The outer opening of

the tympanic bulla is known as the **external auditory meatus**. The **Eustachian canal**, leading into the tympanic bulla, passes between the latter and the basisphenoid. Just median to this is the **foramen lacerum medium** for the entry of the internal carotid artery. There is a canal in the alisphenoid, but it is not a true foramen, since it does not enter the skull, the external carotid artery which passes through it penetrating the alisphenoid, in which it runs for some distance before emerging again, still on the outside of the skull. The mandibular branch of V emerges through the **foramen ovale**, situated between the periotic and the alisphenoid. In the alisphenoid itself is the **foramen rotundum**, through which

TABLE I. – BONES OF THE SKULL

Region of skull	Cartilage Bone	Membrane Bone
Floor	Basioccipital Basisphenoid Presphenoid Pterygoids	Vomer
False palate	Palatines	Maxillae
Roof	Supraoccipital	Parietals Frontals Nasals
Side wall	Periotic Alisphenoid Orbitosphenoid	Squamosal Lachrymal Tympanic
Upper jaw		Premaxilla Maxilla
Lower jaw		Dentary
Zygomatic arch		Jugal Squamosal
Ear ossicles	Stapes Incus Malleus	

TABLE II. – FORAMINA OF THE SKULL

Foramen	Position	Structure passing through
F. magnum	Posterior end of skull	Spinal cord
Condylar f.	In exoccipital	Nerve XII
F. lacerum posterius	Between periotic and exoccipital	Nerves IX, X, XI and internal jugular vein
Stylo-mastoid f.	Between tympanic bulla & periotic	Nerve VII
F. lacerum medium	Between tympanic bulla & basisphenoid	Internal carotid artery
Eustachian canal	Between tympanic bulla & basisphenoid	Eustachian tube
F. ovale	Between alisphenoid & periotic	Mandibular branch of V
F. rotundum	In alisphenoid	Maxillary branch of V
F. lacerum anterius	Between orbitosphenoid & alisphenoid	Nerves III, IV, VI and ophthalmic branch of V
Optic f.	In orbitosphenoid	Nerve II

passes the maxillary branch of V. Between the alisphenoid and the orbitosphenoid lies the **foramen lacerum anterius**, through which pass nerves III, IV, VI and the ophthalmic branch of V. In the orbitosphenoid bone itself is the **optic foramen** for nerve II.

The upper jaw is formed of a pair of premaxillae and maxillae. From the hind end of each of the latter is a backward-projecting **jugal**, which meets a process of the squamosal to form the **zygomatic arch**. The floor of the cranium is partly shut off from the cavity of the mouth by a false palate. This is formed by inward extension of the maxillae and by the palatines, continuous behind with them. Each meets the corresponding bone from the other side in the middle line. In this way a separate nasal passage is cut off from the general cavity of the mouth. Just behind each palatine is a small **pterygoid**.

The lower jaw contains only one bone, known as the **dentary**, articulating with the squamosal.

The inner opening of the auditory capsule, the **fenestra ovalis**, is connected with the tympanum by a chain of three bones, known as the ear ossicles. They are the **stapes** (next to the fenestra ovalis), the **incus** and the **malleus**, abutting on to the tympanum. They are respectively homologous with the columella auris, the quadrate and the articular of lower forms.

The only other portion of the visceral skeleton surviving is the hyoid. It consists of a median plate of bone and two pairs of backward projecting cornua. A pair of small anterior cornua connect the hyoid with the periotic. The thyroid, cricoid and arytenoid cartilages of the larynx constitute the remainder of the splanchno-cranium.

The main characters of the skull may be summarised by the two tables on page 150, dealing respectively with the bones comprising the skull and the foramina pierced in or between them. The diagram of the skull shown in Fig. 104 will help in remembering the positions and nature of the bones.

Internal Anatomy

As with the frog the organs of the rabbit are segregated into a number of distinct systems, each of which will be described individually.

Alimentary System

The margin of both jaws is bordered by a single layer of teeth. These, unlike those of the frog, are of different types. Thus the dentition of the rabbit and of mammals in general is described as **heterodont**, whereas that of lower Chordata is homodont, all the teeth being alike. The front teeth of the mammals are known as the **incisors**, and are sharp-edged for cutting. Those of the upper jaw are four in number in the rabbit, and are set two in each premaxilla. In the lower jaw there are two incisors, one on either side of the middle line. In the rabbit there is a long, toothless space

on each side in both jaws immediately behind the incisors. This is known as the **diastema**. In most animals, and especially in carnivorous forms, this is occupied by **canine** teeth, one in each space. These are well developed in the dog, and are the first teeth on the maxillae. Behind the diastema in each jaw of the rabbit lie the double teeth, regionally differentiated into **premolars** in front and **molars** behind. In the dog the last premolar on each side in the upper jaw and the first molar in the lower is particularly large: these four are termed **carnassial** teeth. Now mammals characteristically have only two generations of teeth, the deciduous teeth of the young being later replaced by a permanent set. This

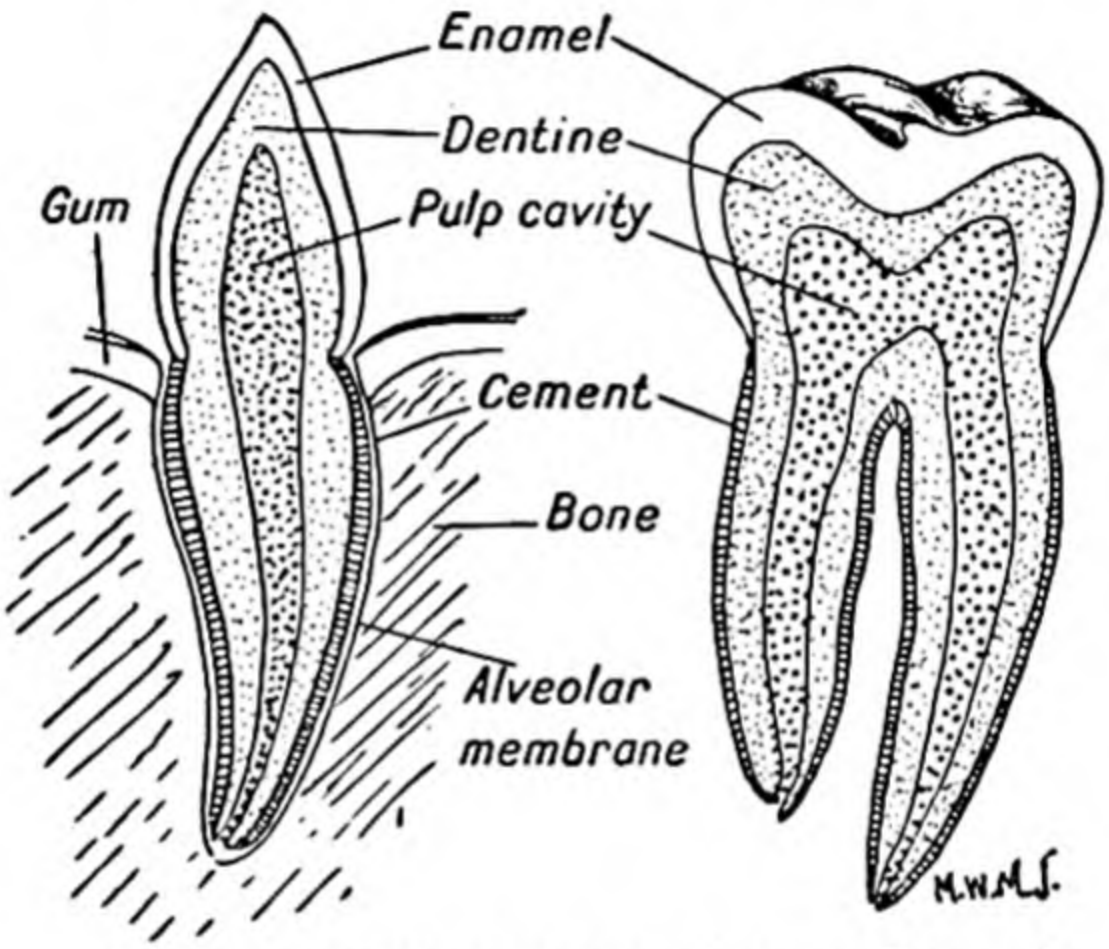


FIG. 105 – Vertical sections of mammalian teeth.

condition is described as **diphyodont**, in contrast to the polyphyodont condition in lower vertebrates, where there is continuous replacement of teeth throughout life. The premolar teeth can be distinguished from the molars in mammals only by the fact that the latter are not represented at all in the deciduous set, there being only one generation of molars. The numbers of various types of teeth may be clearly and simply represented by means of a **dental formula**. This takes the form of a fraction, the numerator of which represents one side of the upper jaw and the denominator one side of the lower jaw. The digits, reading from left to right, indicate respectively the numbers of incisor, canine, premolar and molar teeth in that order. In order to ascertain the number of teeth in the mouth the digits are all added together and the resultant total multiplied by two. Thus the dental formula of the rabbit is:

$$\frac{2033}{1023},$$

whilst that of dog is:

$$\frac{3142}{3143}.$$

The incisor teeth of the rabbit are peculiar in that they grow perpetually throughout life. They differ from most mammalian teeth in that their pulp-cavities remain open and thus the teeth are continuously supplied with nourishment. They are described as having persistent pulps. Those of each jaw are worn down by rubbing against those of the other jaw during the rabbit's characteristic 'nibbling' of food. The loss of an incisor tooth may well prove fatal to a rabbit, since the one normally grinding against it would continue to grow unchecked.

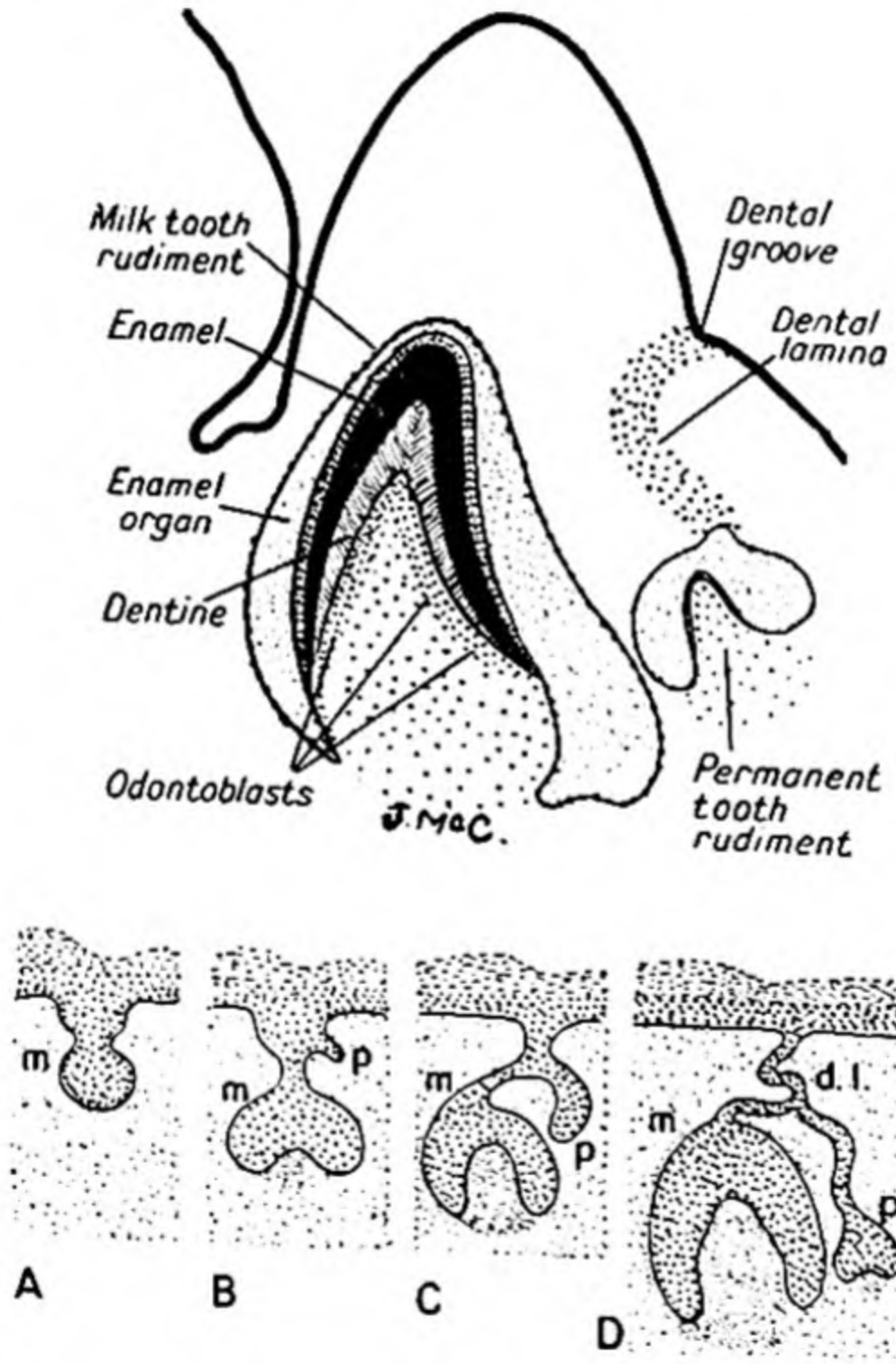


FIG. 106 – *Upper.* Diagrammatic vertical section through jaw to show the development of a tooth.
Lower. A simplified series to show the sequence of events in the formation of a tooth-rudiment.
d.l., dental lamina; *m.*, *p.*, rudiments of deciduous and permanent tooth respectively.

The relationship between dentition and the type of diet upon which the animal feeds is both interesting and important. In the rabbit, which is herbivorous, the protruding and sharp incisors are used for cutting, whilst the diastema allows food from the buccal cavity to be passed into the cheek pouches for temporary storage. This behaviour is very common amongst the relatively defenceless herbivores, for it is essential for them to collect their food in the shortest possible time, during which they are exposed to attacks by predatory carnivores, and subsequently to retreat to comparative safety to masticate it. Thus many herbivores 'chew the cud'. In the rabbit the ridges of the double teeth are harder than the grooves, thus maintaining a rough grinding surface.

In the sheep, which is also herbivorous, the dental formula is:

$$\frac{0033}{3133}$$

The lower incisors are sharp and chisel-like, projecting to grip the grass against a hard pad in the upper jaw. A mouthful of grass is gripped by a twist of the tongue, held firmly as indicated above and torn off with a jerk of the head. The single canine of the lower jaw is in every way indistinguishable from the incisors. Grinding is assisted by the sloping surfaces of the double teeth, those of the upper jaw sloping inwards and those of the lower outwards.

The incisor teeth of the dog, a typical carnivore, are sharp and slightly spaced. They serve for cutting, biting, scraping of meat from bones and for the removal of fur. The canines are characteristically very large and serve for the shredding of flesh. The premolars remain sharp for further cutting, whilst the molars are cusped for crushing and grinding of bone. The carnassial teeth (see above) serve for shearing through flesh and bone and also for the close scraping of meat from bones.

The structure and development of teeth may well be considered at this point. The tooth is externally divisible into three regions – the **crown**, projecting above the gum, the **root**, embedded in the bone of the jaw, and the **neck**, connecting the other two. The bulk of the tooth consists of **dentine**. This is covered in the crown region by a cap of hard **enamel**, and in the neck and root regions by a substance known as **cement**. *Enamel*, which is the hardest substance in the body, is composed of elongated, hexagonal prisms, slightly curved and set vertically upon the surface of the dentine. The prisms are traversed by bridges of inter-prismatic substance. *Dentine* is essentially bone-like in structure, but possesses no Haversian canals or lacunae. It contains many fine, spirally-coursing, branched canaliculi, extending outwards from the pulp cavity, whilst the inter-tubular substance is fibrous. *Cement* likewise is of bony structure and, except where it is very thin, contains both lacunae and canaliculi: there are, however, no Haversian canals. The centre of the tooth is occupied by a space containing nerves and blood-vessels and known as

the **pulp cavity**, the base of which becomes very restricted. The socket into which the tooth fits is termed the **alveolus**, and is lined by the **alveolar membrane**. This is actually a continuation of the periosteum (see page 326) of the jaw-bone.

In origin the tooth is a composite structure. An infolding of the Malpighian layer of the epidermis constitutes the **dental lamina**, whose position is denoted along the surface of the gum by a linear depression, termed the **dental groove**. An evagination of the dental lamina on its outer side gives rise to the **enamel organ** of the tooth, and enamel is secreted from its inner surface, as shown in Fig. 106. Meanwhile mesoderm cells, known as **odontoblasts**, invade the cavity below the enamel organ, and there, except in the centre, they deposit dentine. Ultimately the tooth and the bone come to lie in juxtaposition, and the tooth is forced to the surface by changes in the underlying tissues. The base of the dental lamina subsequently gives rise, in a similar manner, to the permanent tooth, which displaces its deciduous predecessor.

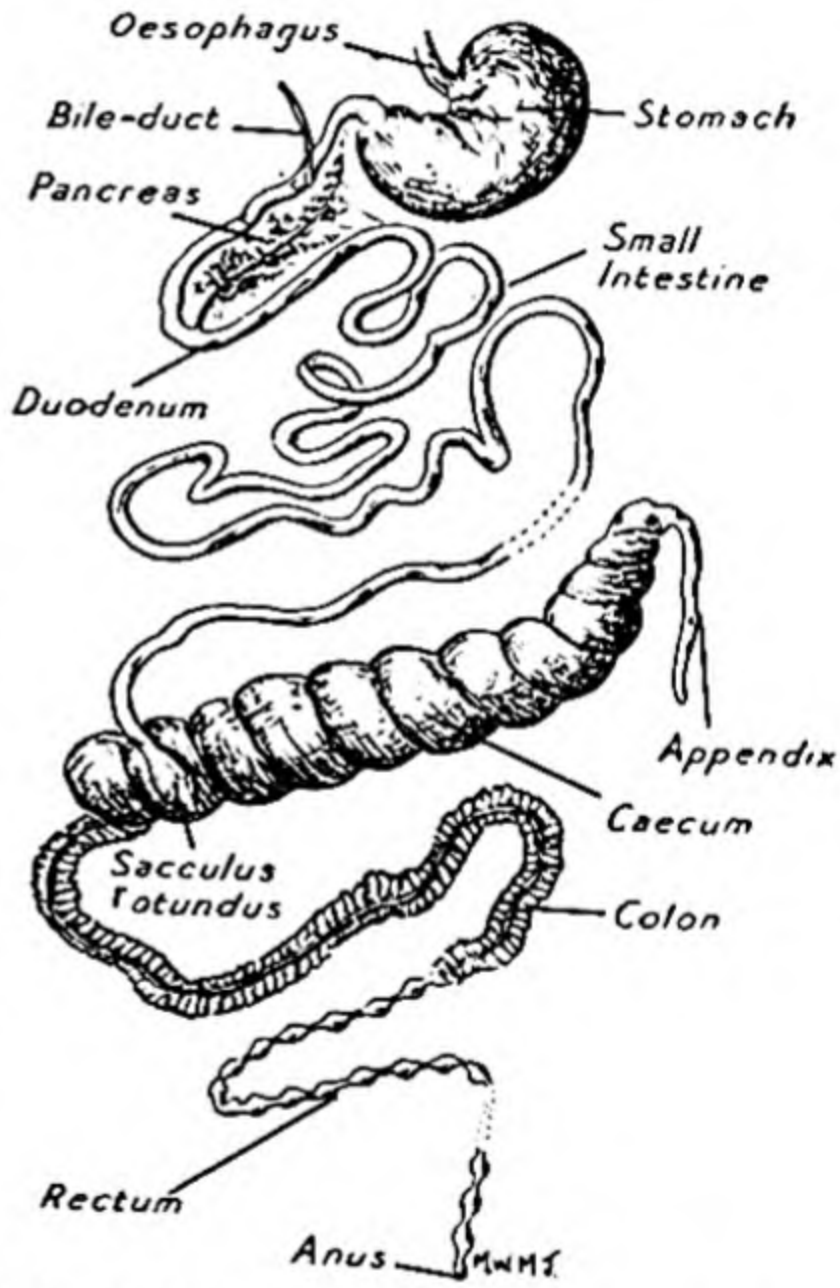


FIG. 107 - *Oryctolagus*. Abdominal portion of the Alimentary canal.

The mouth itself is bordered by a pair of fleshy lips, whilst inside is set a **tongue**. The false palate of bone already referred to (page 151) is continued by a soft palate of non-bony material, so that the nasal cavity opens far back into the dorsal side of the mouth, its opening being known as the **secondary choana**. Adjacent to various parts of the buccal cavity are four pairs of salivary glands, known respectively as the parotid, sub-lingual, sub-maxillary and infra-orbital. They discharge saliva along short ducts into the buccal cavity. From the mouth a narrow tube, the oesophagus, leads to the stomach, passing on its way through the diaphragm. The stomach itself is a large, sac-like organ lying across the body-cavity just beneath the diaphragm. At its distal (pyloric) end it opens into a narrow, U-shaped duodenum, the opening being closeable by a sphincter muscle. The duodenum leads into a long, spirally-coiled intestine, being some seven feet in length and ending in a swelling known

as the **sacculus rotundus**. From this there arises a blind diverticulum, known as the **caecum**, which ends in the form of a narrow **appendix**. The gut itself is continued from the sacculus rotundus in the form of a wide, sacculated colon, leading into a narrow rectum, which communicates with the exterior by an anus.

Separate from the gut but communicating with it by ducts are two important digestive glands – the liver and the pancreas. The **liver** is a large, red organ, subdivided into five lobes. In the posterior end of the right central lobe lies the gall-bladder, communicating by the bile-duct with the duodenum, not far beyond the pyloric sphincter muscle. The whole liver is attached by a **falciform ligament** to the diaphragm. The **pancreas** is a pinkish organ situated between the two arms of the duodenum, where it is supported by a fold in the peritoneum. It opens by a pancreatic duct into the distal limb of the duodenum, a short distance beyond the bend.

The process of digestion is described in Chapter 23. In this connexion it is important to notice the presence of finger-like processes in the lining of the intestine, each being known as a **villus**. Along the lining of the intestine lie areas of specialised lymphatic tissue (page 162), known as **Peyer's patches**, associated with absorption of food.

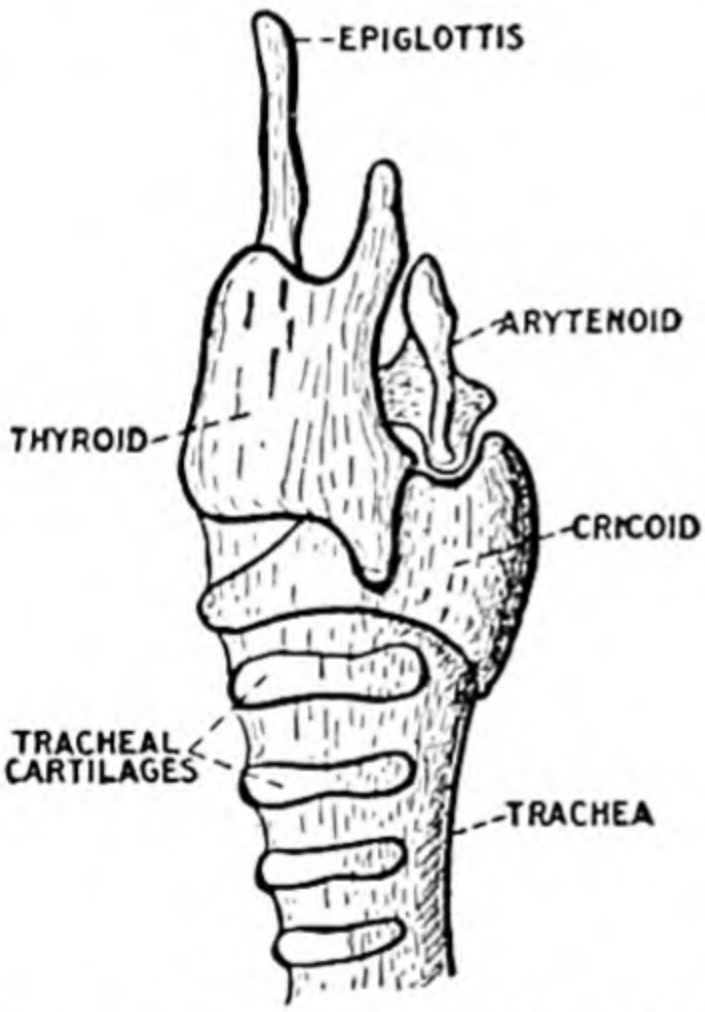


FIG. 108 – The mammalian larynx. (From 'Animal Biology', by A. J. Grove and G. E. Newell. University Tutorial Press.)

Respiratory System

The respiratory organs of the rabbit consist of a pair of lungs, lying in a closed cavity, or **thorax**. This is bordered all round by the body-wall, strengthened in this region by the ribs, whilst it is shut off from the remainder of the coelom by a muscular plate, lying transversely across the body-cavity, known as the **diaphragm**. From the nostrils a nasal chamber leads backwards, opening into the posterior part of the buccal cavity by the secondary choana. Here it meets the oesophagus in a region known as the **pharynx**. The **trachea**, or windpipe, then passes ventral to the oesophagus through the neck. The upper part of the trachea is known as the **larynx**. It is supported by two hoops of cartilage, known as the **thyroid** and **cricoid**, and contains the vocal cords. These take the form of two pairs of membranes between the thyroid and arytenoid cartilages. The anterior pair are the false vocal cords and the posterior pair the true

ones. The openings of the larynx into the pharynx is protected by a flap of cartilage, known as the **epiglottis**. In swallowing this serves to close the opening of the larynx and thus prevents the passage of food into the trachea. An Eustachian tube opens into the cavity of the mouth on either side of the secondary choana, whilst just behind these openings are the **tonsils**, themselves remnants of a second pair of gill-pouches. The anterior end of the trachea is supported by a hoop of cartilage, known as the **arytenoid**. At its base the trachea forks into two **bronchi**. Each of these passes into a lung, where it becomes very much subdivided, first into **bronchioles**, and finally into small, dilated air-sacs, bearing **alveoli**. These are minute dilatations of the surface of the air-sacs, and each is covered by a network of capillaries. Its wall is thin and delicate, permitting gaseous diffusion. The whole structure is bound together into a solid mass by connective tissue. Thus the lungs of the rabbit differ markedly from those of the frog, for the latter are little more than hollow sacs, whose lining is to some extent thrown into folds. The mechanism of respiration in the rabbit is described in Chapter 24.

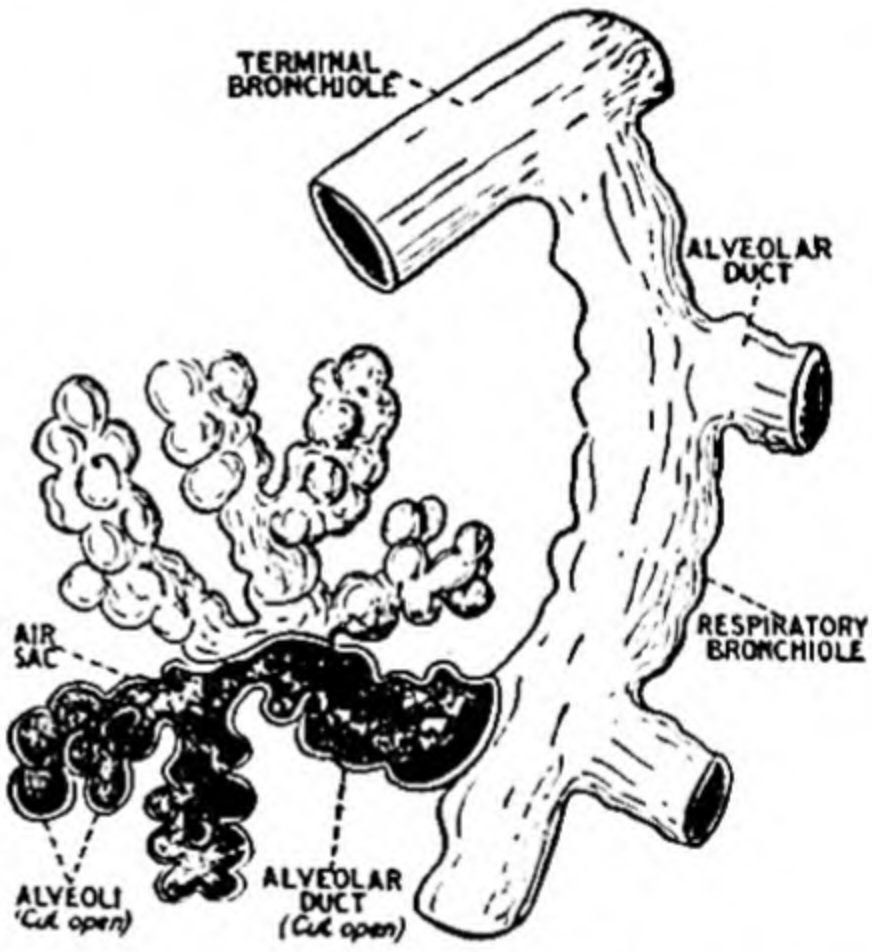


FIG. 109 – Bronchioles and alveoli. (From 'Animal Biology', by A. J. Grove and G. E. Newell. University Tutorial Press.)

Vascular System

This is on the same plan as that of the frog, but the separation of oxygenated from de-oxygenated blood within the heart is efficiently carried out, since the ventricle, a single structure in the frog, is here completely divided into right and left halves.

(A) HEART. The heart contains four chambers, namely a **right** and **left auricle** and a **right** and **left ventricle**. Into the right auricle open the three great veins, returning blood from all parts of the body except the lungs. The left auricle receives the conjoined pulmonary veins from the lungs. Each auricle is in communication with the ventricle of its own side, but the right and left halves of the heart are completely shut off from each other. In the centre of the inter-auricular septum is a depression, known as the *fossa ovalis*. In 'hole-in-the-heart' babies this is actually perforated. The right ventricle is thick-walled but even so is not as thick as the left. From it emerges the pulmonary aorta to run to the lungs. The left ventricle has very thick and

muscular walls, and from it arises the systemic aorta, along which blood passes for distribution to all the tissues of the body, except those of the lungs. As in the frog the various apertures between the chambers of the heart and the vessels communicating with it are guarded by valves. A **tricuspid** valve guards the right auriculo-ventricular aperture, whilst the base of the pulmonary artery is guarded by three **semi-lunar** valves. The

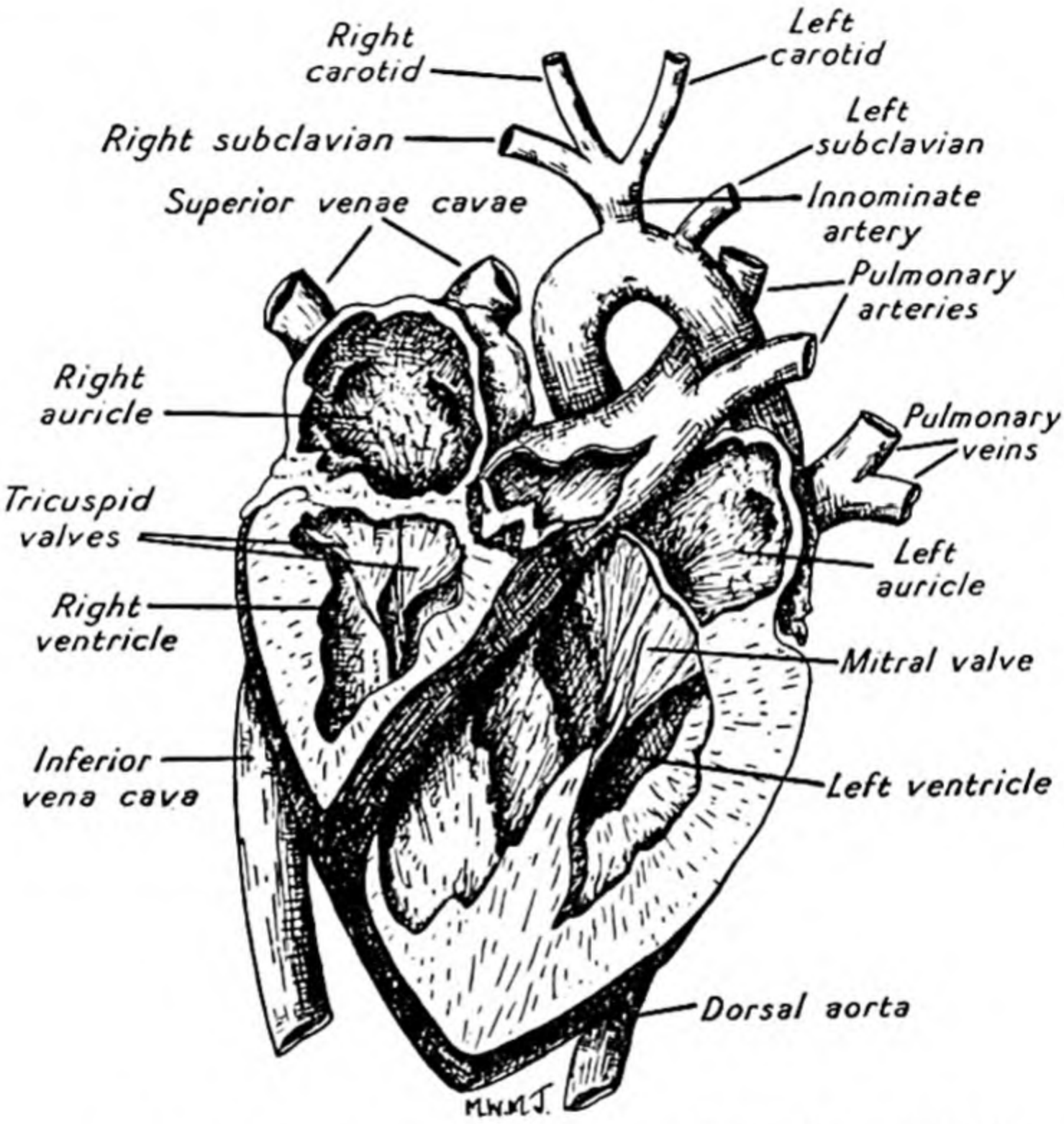


FIG. 110 – *Oryctolagus*. The heart, dissected from the ventral side.

mitral valve is found at the left auriculo-ventricular aperture, and differs from the tricuspid in that it consists of only two membranous folds. The base of the aorta is set with three **semi-lunar** valves.

Thus the general course of blood-circulation in the rabbit may be summarised as in Fig. 113.

(B) ARTERIAL SYSTEM. The **aorta** leaves the left ventricle, curves to the left and then passes backwards to run dorsal to the apex of the heart, from which point onwards it is termed the **dorsal aorta**. Shortly

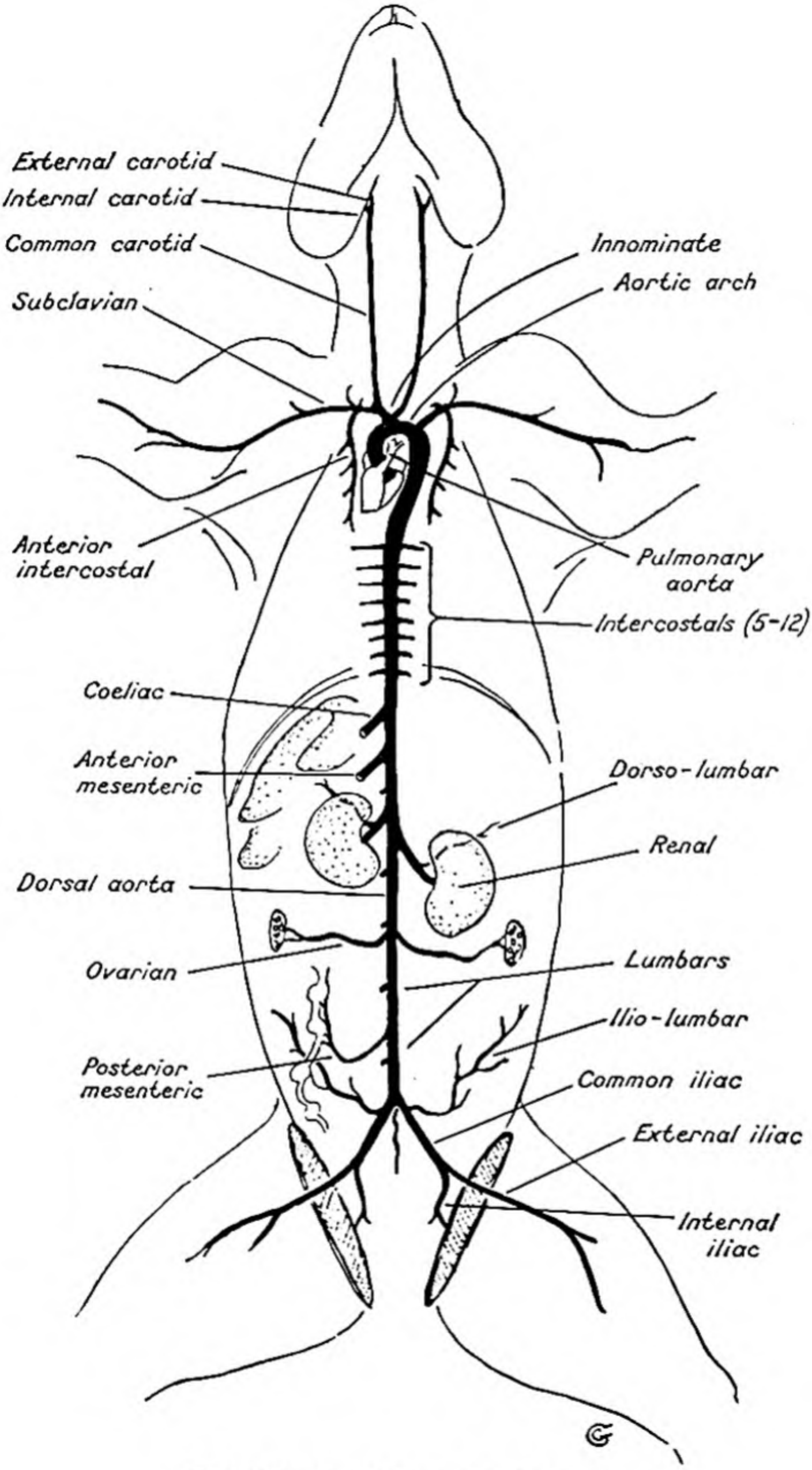


FIG. 111 – *Oryctolagus*. Arterial system.

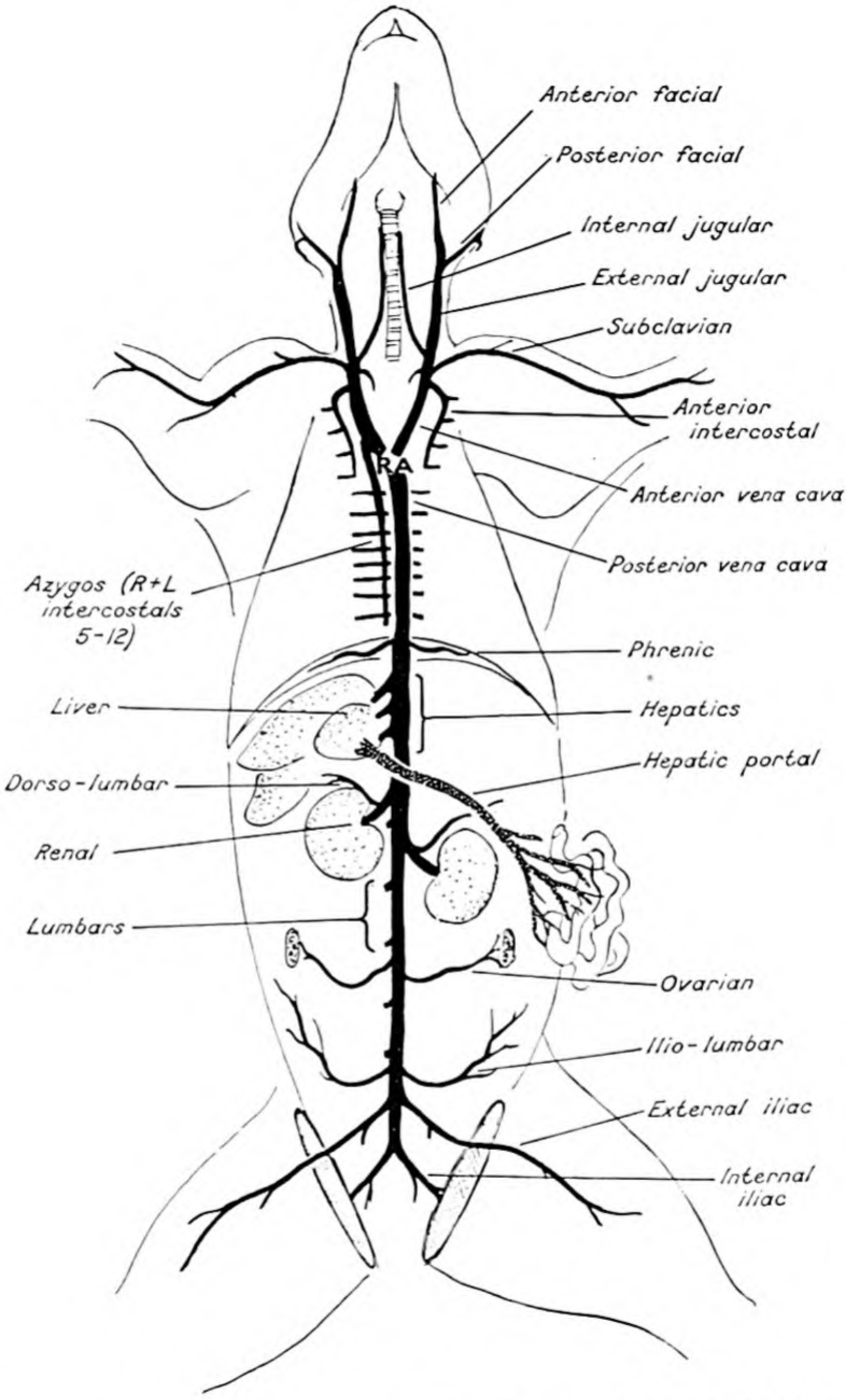


FIG. 112. *Oryctolagus*. Venous system. (The pulmonary veins have been omitted.)

after leaving the heart it gives off a **coronary** artery to supply the wall of the heart itself, followed by a short **innominate** artery, which forks to form right and left **common carotid** arteries, the *right* of which gives off a **subclavian** artery. The *left* subclavian arises directly from the aortic arch, shortly after the innominate, and passes into the left arm. The aorta then comes to run in the mid-dorsal line and in its passage along the back gives off **inter-costal** arteries to the musculature of the chest, and a **coeliac** artery, which divides to form a hepatic to the liver and a lieno-gastric to the spleen and stomach. Behind it arises a median **anterior mesenteric**, and laterally at much the same level the **right renal** artery is given off. The **left renal**, in accordance with the asymmetric position of the rabbit's kidneys, arises more posteriorly. Farther back arises a median **posterior mesenteric**, as well as a pair of arteries (**spermatic** or **ovarian**) to the testes or ovaries. Behind these the dorsal aorta bears a pair of **lumbar** arteries, each further subdivided into three branches – the *dorso-lumbar*, the *median segmental* and the *ilio-lumbar*. At its hind end the dorsal aorta gives off an **iliac** artery to either leg, whilst it itself is continued into the tail as the slender **caudal** artery. From the right ventricle arises the **pulmonary** artery. This divides into two, one branch passing to either lung.

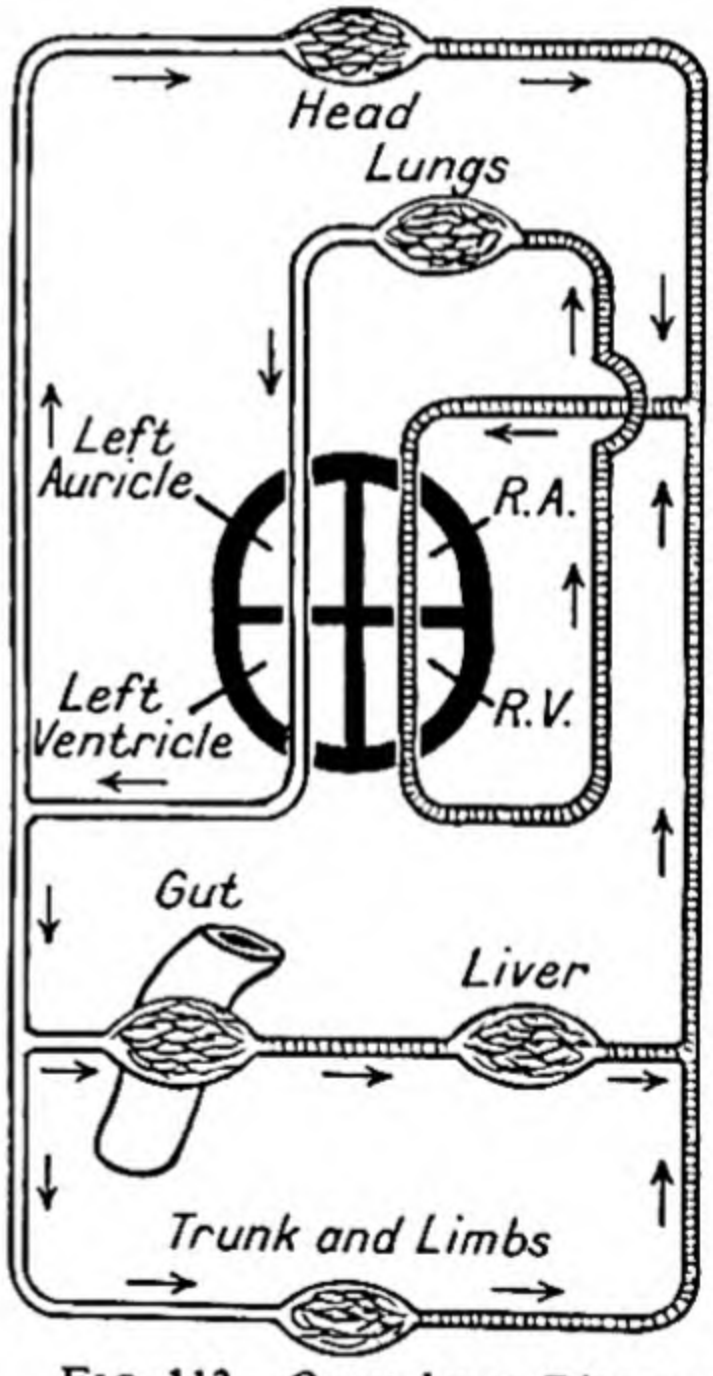


FIG. 113 – *Oryctolagus*. Diagram to represent the course of circulation of the blood.

A point of evolutionary significance in respect of the blood system is a ligamentous band, the **ductus arteriosus**, connecting the aorta with the left pulmonary artery. The significance of this structure is discussed on page 539. It is to be noted here that the red corpuscles of mammalian blood are biconcave and enucleate.

(C) VENOUS SYSTEM. Unlike the frog and dogfish the rabbit has no sinus venosus. This organ is represented in a vestigial condition by a sino-auricular node, the so-called pace-maker of the heart, since it is through stimulation of this region that the rate of heart-beat is regulated. De-oxygenated blood is returned from all parts of the body by three great veins, opening independently into the right auricle. Each of the two **anterior venae cavae** consists of a conjoined **subclavian** and **jugular** vein, the latter being formed from a

small internal and large external branch. A further vessel is often to be observed, running transversely and connecting the two external jugular veins, just anterior to their junction with the internal jugulars: this vessel is the **jugular anastomosis.** The right anterior vena cava receives the **azygos** vein from the wall of the thorax of its own side, as well as the **anterior intercostal**, also draining blood from the wall of the thorax. On the left an **anterior intercostal** is similarly disposed, whilst a small **hemiazygos** may be present, corresponding to the larger azygos on the right. **The posterior vena cava** itself receives many branches on its journey to the heart. Each leg is drained by an **external** and an **internal iliac** vein, whilst blood from the pelvic region of the body-wall is collected into paired **ilio-lumbars**. **Spermatic** or **ovarian** veins return blood from the genital organs, whilst a pair of asymmetrically-placed **renal** veins communicate with the kidneys. Blood from the liver is passed into the posterior vena cava by the **hepatic** veins.

There is no renal portal system in mammals, but blood is conveyed from the stomach and intestine to the liver via a **hepatic portal** vein, which becomes subdivided to form very small sinusoids within the tissues of the liver so that carbohydrate food may be extracted and stored as glycogen.

Lymphatic System

Much of the dissolved food finds its way into the lymph-vessels associated with the great veins of the body. The majority of lymph-vessels eventually open into the **thoracic duct**, communicating with the left subclavian vein near its union with the jugular vein. The lymphatic vessels from the right side of the anterior part of the body open into the right anterior vena cava.

Nervous System

The general classification of the nervous system into its component parts is the same as that of the dogfish (page 97). It is principally in respect of the brain that specialisation has occurred, and in the mammal this organ shows a very considerable advance on anything previously encountered.

(A) BRAIN. This organ may be subdivided into the same five parts as that of the frog. The **telencephalon** consists of a pair of very much enlarged cerebral hemispheres, extended backwards completely to cover the mid-brain. Each hemisphere is subdivided superficially into a number of lobes by fissures. Laterally at about the middle of its length occurs a **Sylvian fissure**, dividing a posterior temporal lobe from the remainder, whilst ventrally a longitudinal **rhinal fissure** separates a **rhinencephalon** towards the middle line from the frontal (anterior) and temporal (posterior) lobe laterally. The rhinencephalon itself is transversely divided into an anterior **olfactory** lobe and a posterior **hippocampal** lobe.

The former is continued forwards to end in a small olfactory bulb. The two cerebral hemispheres are connected by a transverse band of fibres, known as the **corpus callosum**, a development peculiar to mammals.

The side walls of the **diencephalon** are very thick, forming the optic thalami. These are in contact in the centre, forming the so-called 'soft commissure', thus constricting the cavity of the third ventricle. The floor

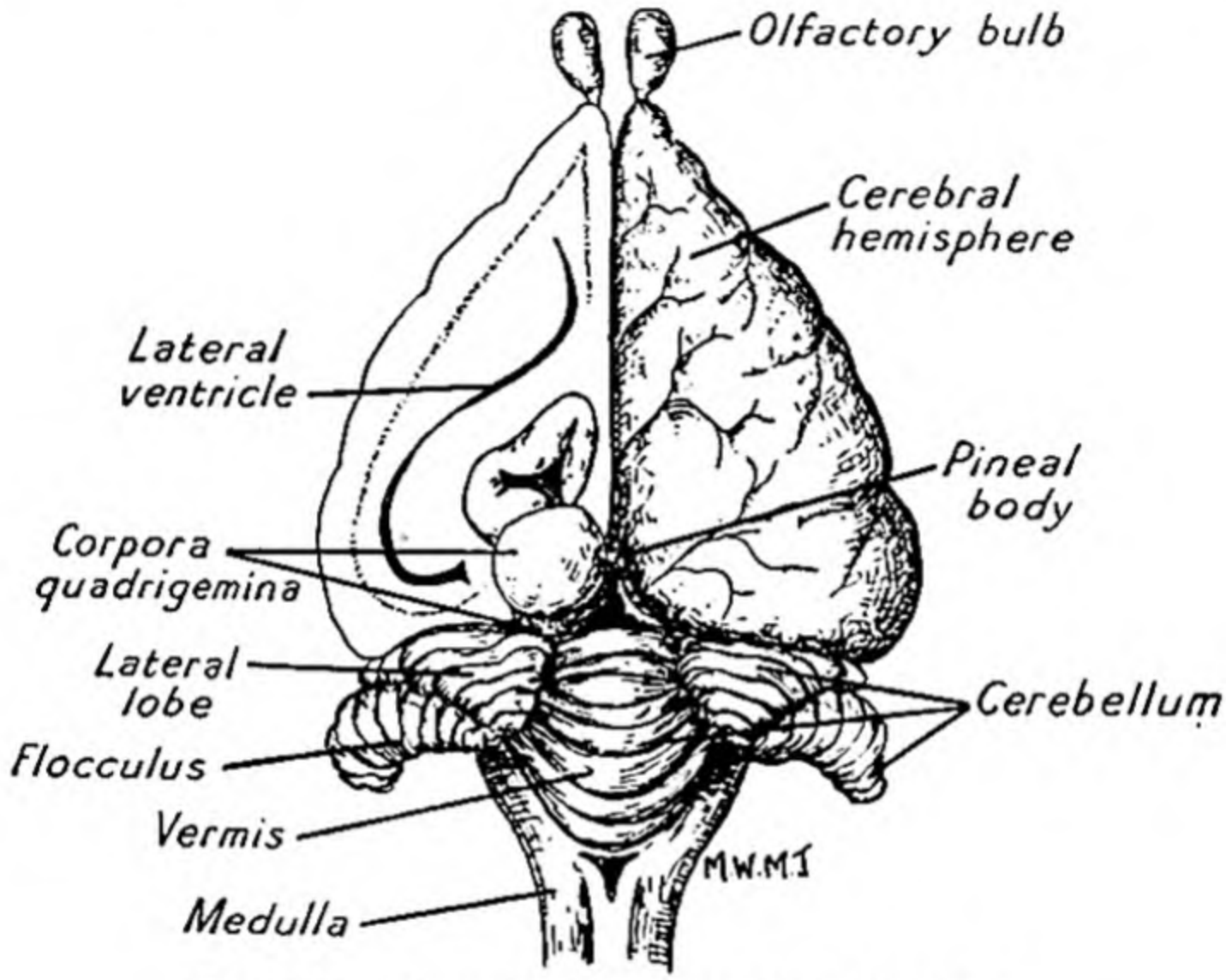


FIG. 114 – *Oryctolagus*. Dorsal view of the brain.

of this part of the brain bears the infundibulum, associated with the hypophysis to form the pituitary body, whilst from the roof projects a pineal stalk, ending in a pineal gland. On either side of the infundibulum is a longitudinal band of fibres, constituting the **crura cerebri**, whilst the swollen end of a backward extension of the stalk of the pituitary body forms the **corpus albicans**.

Whereas the roof of the **mesencephalon** of the frog is thickened and expanded to form only two optic lobes, these organs have each become divided into two in the mammal, the resultant structures being known as the **corpora quadrigemina**. The nerve tracts from these structures pass forwards to cross within the floor of the hind end of the telencephalon, forming the optic chiasma (see also page 470). The side walls of the mesencephalon are formed by the crura cerebri.

In the **metencephalon** the much folded cerebellum has become enlarged and subdivided into a median **vermis** and two lateral lobes. To the outer side of each lateral lobe occurs a small **flocculus**. The superficial layer

(cortex) of the two sides of the cerebellum is connected by a band of transverse fibres, passing ventral to the rest of the brain and known as the **pons Varolii**.

The **myelencephalon**, or medulla oblongata, much thickened ventrolaterally, gradually narrows posteriorly to pass into the spinal cord.

The cavities of the brain are named as for the frog (page 131). The lateral ventricles each communicate with the cavity of the diencephalon (the third ventricle) by a foramen of Monro. The cerebellum itself is solid, for the cavity of the fourth ventricle does not extend into it.

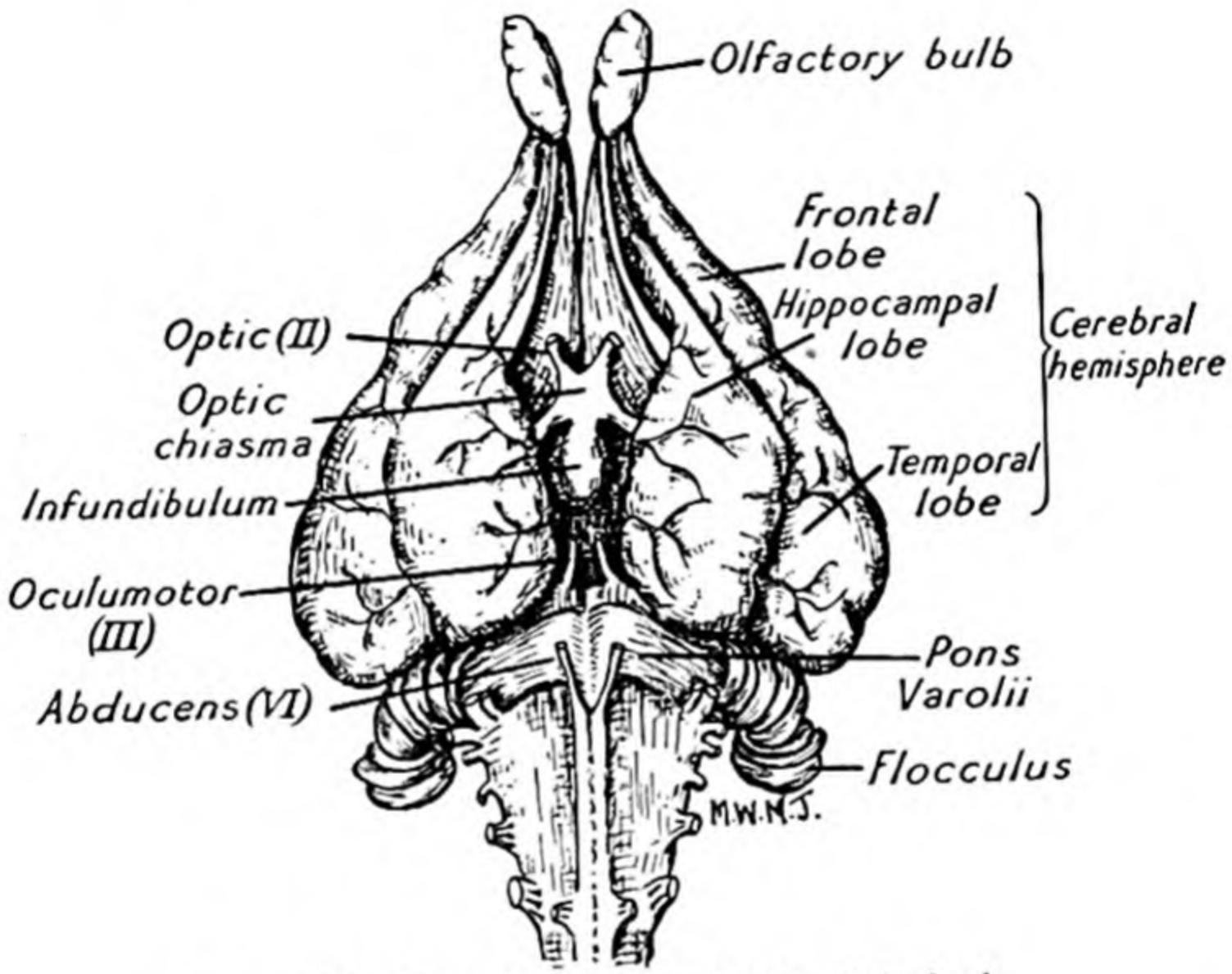


FIG. 115 – *Oryctolagus*. Ventral view of the brain.

The brain is enclosed in membranes, collectively known as the **meningeal membranes**. The inner is the pia mater, which is richly vascularised and penetrates the roofs of the fourth and third ventricles to form in each a choroid plexus. It is enclosed in a protective dura mater. Between the pia mater and the dura mater is a third membrane, known as the **arachnoid layer**. The space enclosed between these membranes and the brain is in communication with the cavity of the brain itself by a minute **foramen of Magendie** in the roof of the fourth ventricle.

(B) SPINAL CORD. The structure of the spinal cord is fundamentally similar to that of the frog, described on page 131 and more fully discussed in Chapter 26.

(C) CRANIAL NERVES. There are twelve pairs of cranial nerves in

the rabbit. The first ten pairs are similar in name, and essentially in distribution, to those of the frog. The eleventh pair is the **spinal accessory,** supplying muscles of the neck. The twelfth pair of nerves corresponds to the first spinals of the frog in distribution, and each is thus called a **hypoglossal.**

It is only in the neck that the distribution of cranial nerves in the rabbit differs essentially from that in the frog. The vagus emerges through the

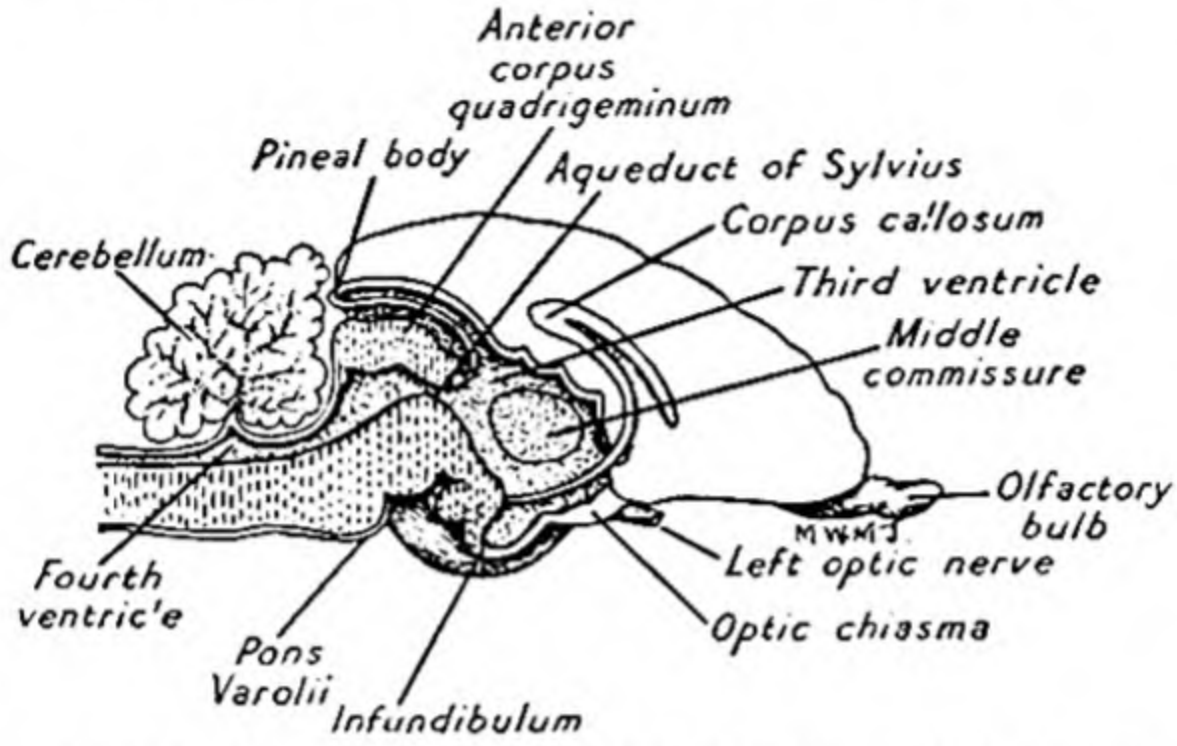


FIG. 116 – *Oryctolagus.* Longitudinal section of the brain.

foramen lacerum posterius and becomes expanded to form a vagus ganglion. Just beyond this ganglion it gives off a **depressor** branch to the heart and an **anterior laryngeal** to the larynx. The main branch of the vagus passes ventral to the aortic arch on the left and to the innominate artery on the right. Each vagus then gives off a **recurrent laryngeal** nerve. The right recurrent laryngeal loops round the innominate artery and that of the left side round the ductus arteriosus, each to run forward again to the larynx. The main branch of the vagus supplies the viscera. The **hypoglossal** (XII) passes on either side posterior to the angle of the jaw and sends backwards a **ramus descendens** to muscles of the neck.

(D) SPINAL NERVES. These are built on essentially the same plan as in *Rana* but are, of course, much more numerous. Branches of the fourth and fifth cervical spinal nerves unite on each side to form a **phrenic** nerve to the diaphragm.

(E) AUTONOMIC NERVOUS SYSTEM. Running on either side of the aorta is a ganglionated autonomic nerve-cord. At each ganglion it receives a **ramus communicans** from the spinal nerve of that segment. It passes forwards, and in the hind end of the neck swells to form a **posterior cervical ganglion.** Dorsal to the vagus ganglion the autonomic nerve-cord bears an **anterior cervical ganglion,** from which it continues forward into the head in company with the internal carotid artery. At the root of both the anterior and posterior mesenteric arteries is a ganglion, supplied

with nerve-fibres from neighbouring autonomic ganglia. These **mesenteric ganglia** in turn innervate the musculature of much of the viscera, including the gut and the bladder. The collection of nerves centred around the anterior mesenteric artery forms the **solar plexus**. The splanchnic nerve to the solar plexus arises by the fusion of elements from the thoracic

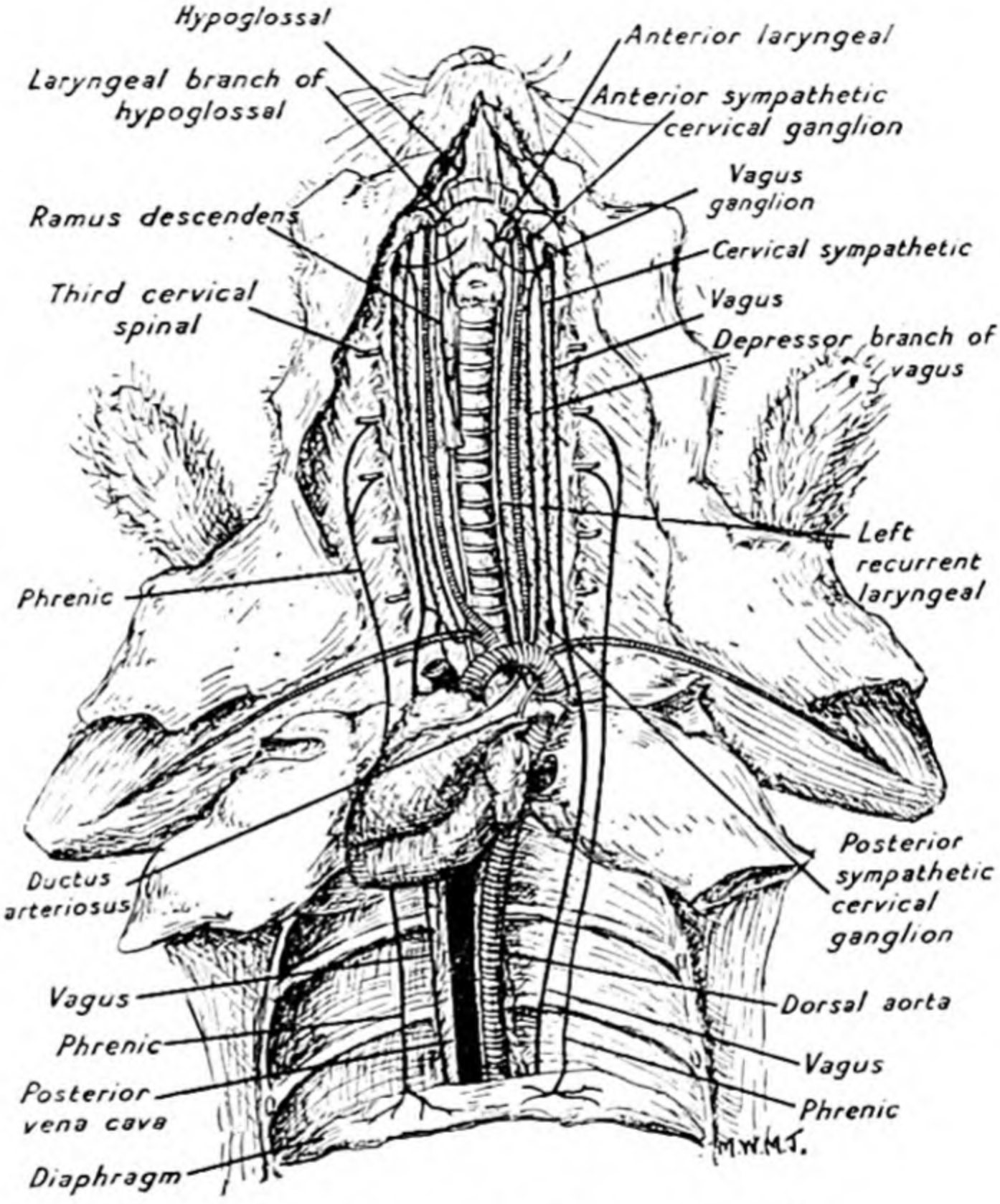


FIG. 117 – *Oryctolagus*. Nerves of the neck.

portion. The components of the autonomic nervous system are more fully described on page 466.

(F) SENSE ORGANS. Both the eye and the ear of the mammal are essentially the same as those of the lower vertebrates, and they will now be separately described.

(i) *Eye*. The mammalian eye, as in all the vertebrates, consists essentially of a hollow vesicle, the wall of which is three-layered. The outermost layer is the **sclerotic**. This is composed of tough connective tissue

and some cartilage and is protective, as well as providing firm ground for the insertion of eye-muscles. Anteriorly it is much thinner and becomes transparent, this region being known as the **cornea**. The sclerotic coat is really comparable with the olfactory and auditory capsules but is separated from the skull, whereas the other capsules are fused with it. Immediately within this is the **choroid** layer. This is vascularised and is

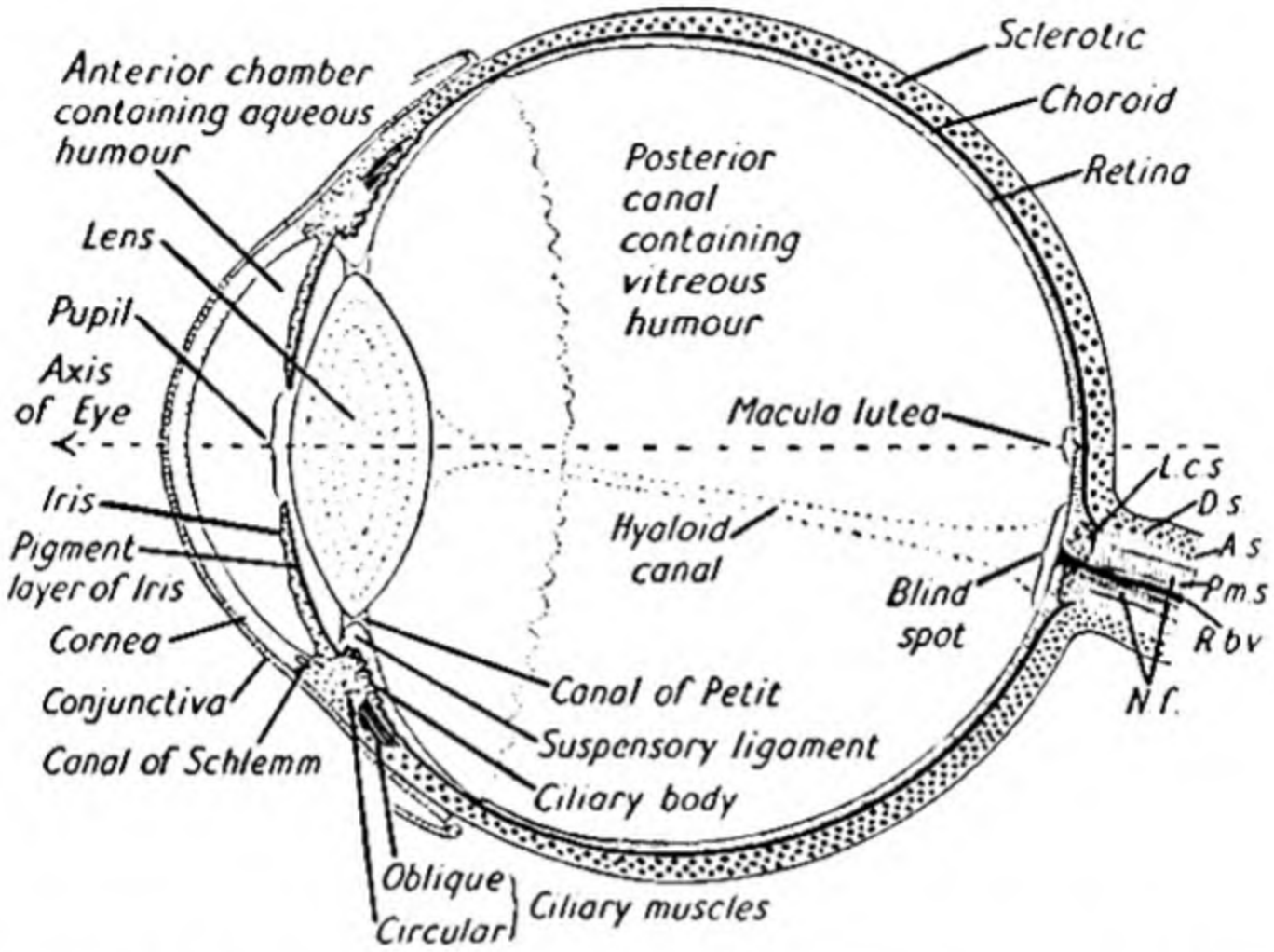


FIG. 118. Diagrammatic median horizontal section through the right human eye. *A.s.*, Arachnoidal sheath; *D.s.*, Dural sheath; *L.c.s.*, Lamina cribrosa sclerae; *N.f.*, Nerve fibres; *P.m.s.*, Pia matral sheath; *R.b.v.*, Retinal blood-vessels.

the nutritive layer of the eye. At the front of the eye the choroid layer is perforated by a circular aperture, and surrounding this aperture is a pigmented disc, known as the **iris**. The aperture itself appears as a black disc – the **pupil**. Arising from the choroid coat, just posterior to the iris, is a circular shelf, known as the **ciliary body**, to which the lens is attached around the whole of its circumference by a **suspensory ligament**. The lens itself is transparent and spherical, and serves to focus light on to the sensitive region at the back of the eye. Together with the ciliary body the lens forms a partition, dividing the cavity of the eye into anterior and posterior chambers. The former contains a watery fluid, known as the **aqueous humour**, whereas the posterior chamber is filled with a more viscous **vitreous humour**. The presence of these liquids reduces the amount of refraction of light as it passes into and out of the lens. The vitreous chamber is traversed by a slender **hyaloid canal**. The ciliary body is attached at its base to the sclerotic coat by the ciliary muscles, whilst

the iris itself contains circular and radial muscles, the contraction of the former reducing the size of the pupil. The innermost layer of the eye is

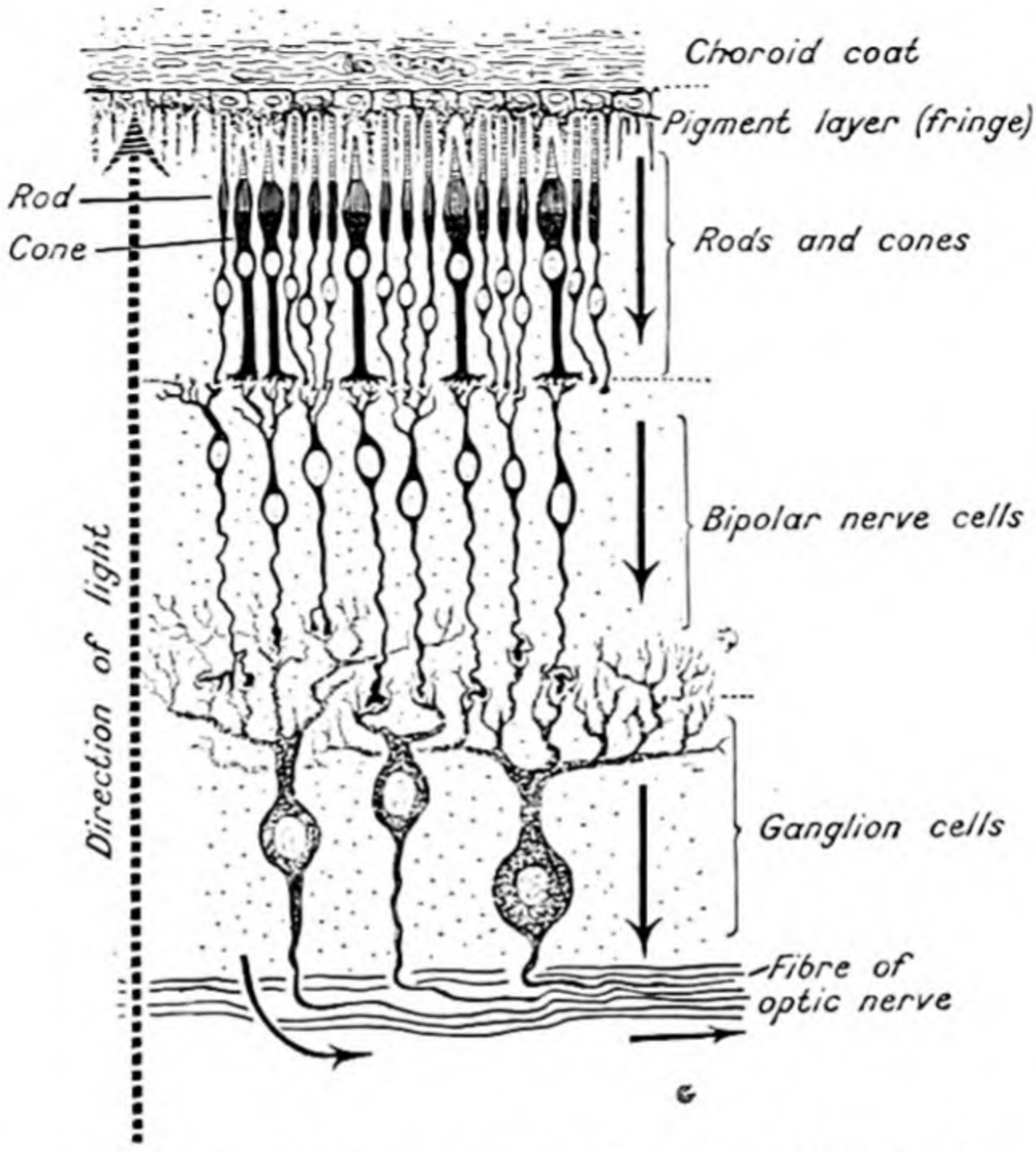


FIG. 119 – Vertical section through the retina. Unbroken arrows show the direction of nerve impulses from the rods and cones. Neuroglial cells between the neurones have been omitted.

the **retina**, and this is the sensitive layer. Its minute structure is described below. The optic nerve enters the eye from behind, and nerve-fibres become spread out over the surface of the retina, which they penetrate by turning backwards.

The retina is divisible into three distinct layers. The innermost is known as the **fringe**, and consists of a single layer of cells, bearing on their inner surfaces cilia-like projections. Of all the layers of the retina this one alone is continued forwards to line the inner surface of the iris. The cells contain granules of a pigment, termed **melanin**. Within the fringe are the photo-receptive cells, which are themselves of two types – the **rods** and the **cones**. Their shapes will be made clear by reference to Fig. 120. The rods and cones are connected at their outer ends – *i.e.* towards the front of the eye – with the fibres of the optic nerve by bipolar nerve-cells, constituting the third layer of the retina. The rods and cones and the bi-polar

nerve-cells are held in position by **neuroglial cells**, whilst most of the surface of the retina is covered by a thin network of blood-vessels.

Finally it should be noticed that the surface of the eye is covered, to the extent shown in Fig. 118, by the transparent **conjunctiva**, which is continuous with the lining of the eye-lid and the epidermis of the face.

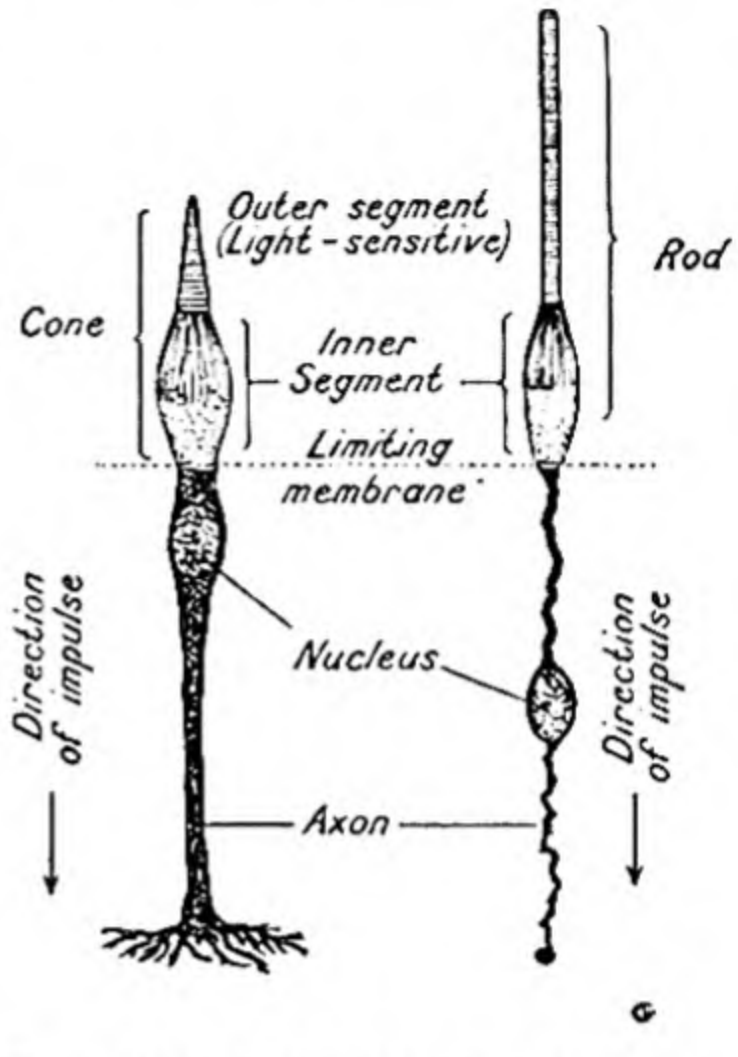


FIG. 120 – Single rod and cone cells.

Physiology of Vision. The physiology of vision may be considered under two distinct heads. The first of these is known as **accommodation**, by means of which images are thrown on to the retina. This is effected by the cornea and the lens. The latter is held within a tough capsule, and when a distant object is being viewed the surface of the lens is flattened by tension in the suspensory ligaments. For near objects the radius of curvature is decreased by contraction of muscles in the ciliary body, whose diameter is thereby decreased. The lens, as a result of its own elasticity, assumes a more spherical shape. Furthermore, the aperture enclosed by the iris diminishes in size, so that light falls only upon the most convex part of the lens.

The second aspect of the physiology of vision concerns the behaviour of the rods and cones. The cones are responsible for colour perception, and are possibly of three types, sensitive respectively to red, green and violet. They are most common at the *fovea centralis*, a sensitive region just to the outer side of the blind spot. They are stimulated only by light of considerable intensity and are therefore operative in bright light (day or artificial). At other times the rods take over (see below). The rods perceive varying intensities of light. Their cylinders produce **rhodopsin** (visual purple), a substance closely allied to vitamin *A*, which, in its turn, can be derived from the plant pigment, carotene. Hence there is some foundation for the belief that carrots, which contain much of this pigment, may be employed as an item of diet to improve powers of vision. When the eye is stimulated by light the rhodopsin is decomposed to form a compound, *retinene*, plus an associated protein molecule. Subsequently retinene, which is of aldehydic nature, is enzymically reduced to vitamin *A*, from which rhodopsin is reconstituted, involving association with the relevant protein. Rods alone exist at the periphery of the retina. In bright light the rhodopsin is destroyed more rapidly than

it can be reconstituted, so that rods are operative only in subdued light.

In mammals only, half the fibres of the optic nerve cross at the optic chiasma, and this results in the nerve-fibres from the right side of *both* retinae running to the one optic lobe, and those from the left to the other. This is probably associated with stereoscopic vision. See page 470.

Although the eye of the dogfish essentially resembles that of the mammal, there are one or two peculiar features worthy of note. Normally focused for distant objects, it is accommodated for near vision by the movement of the lens further from the retina, and not by an increase in convexity. The retina itself consists exclusively of rods, the rhodopsin of which exhibits maximum sensitivity to light of wave-length 505 mμ. It is interesting to note that light of this wave-length is also the most

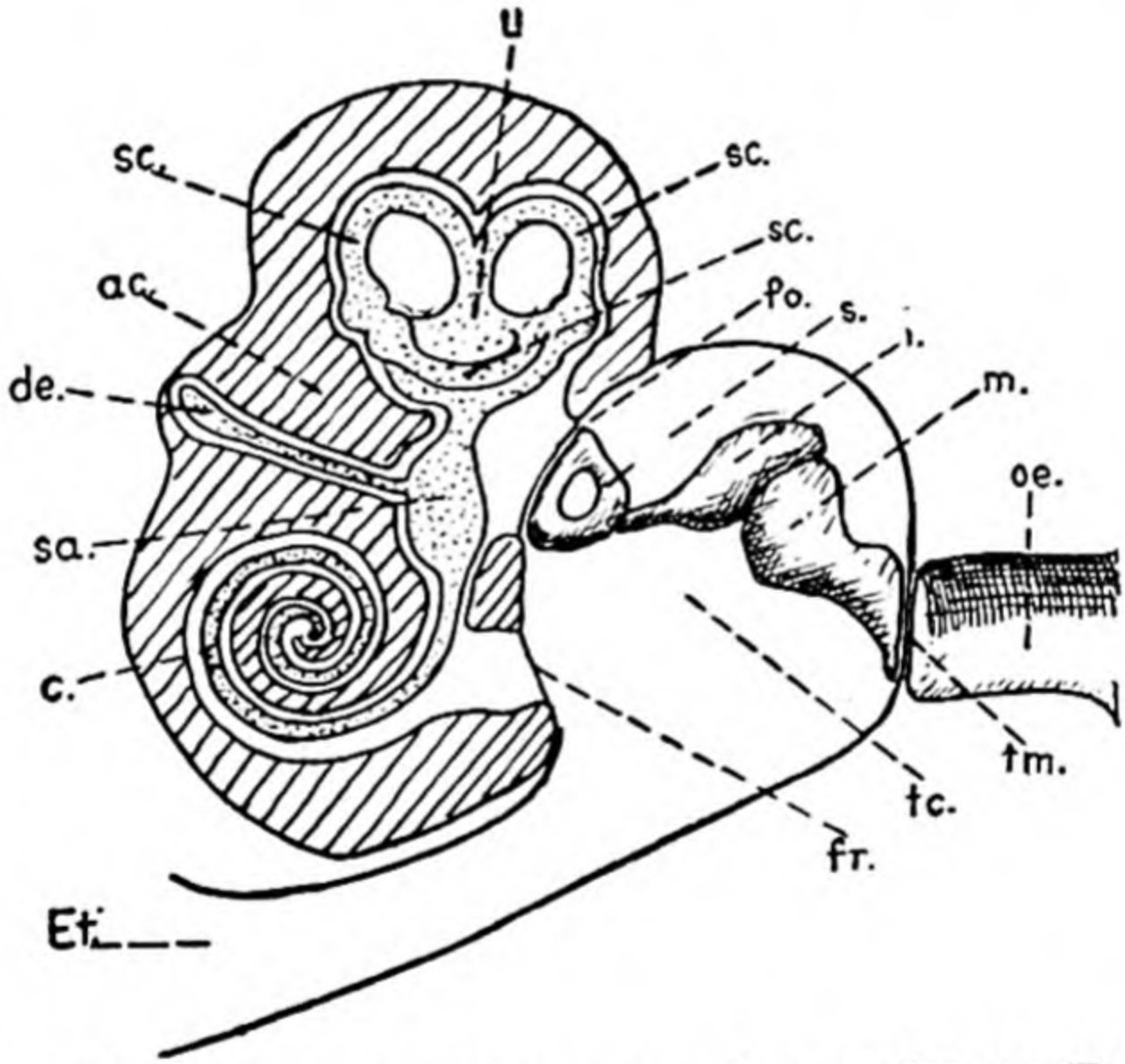
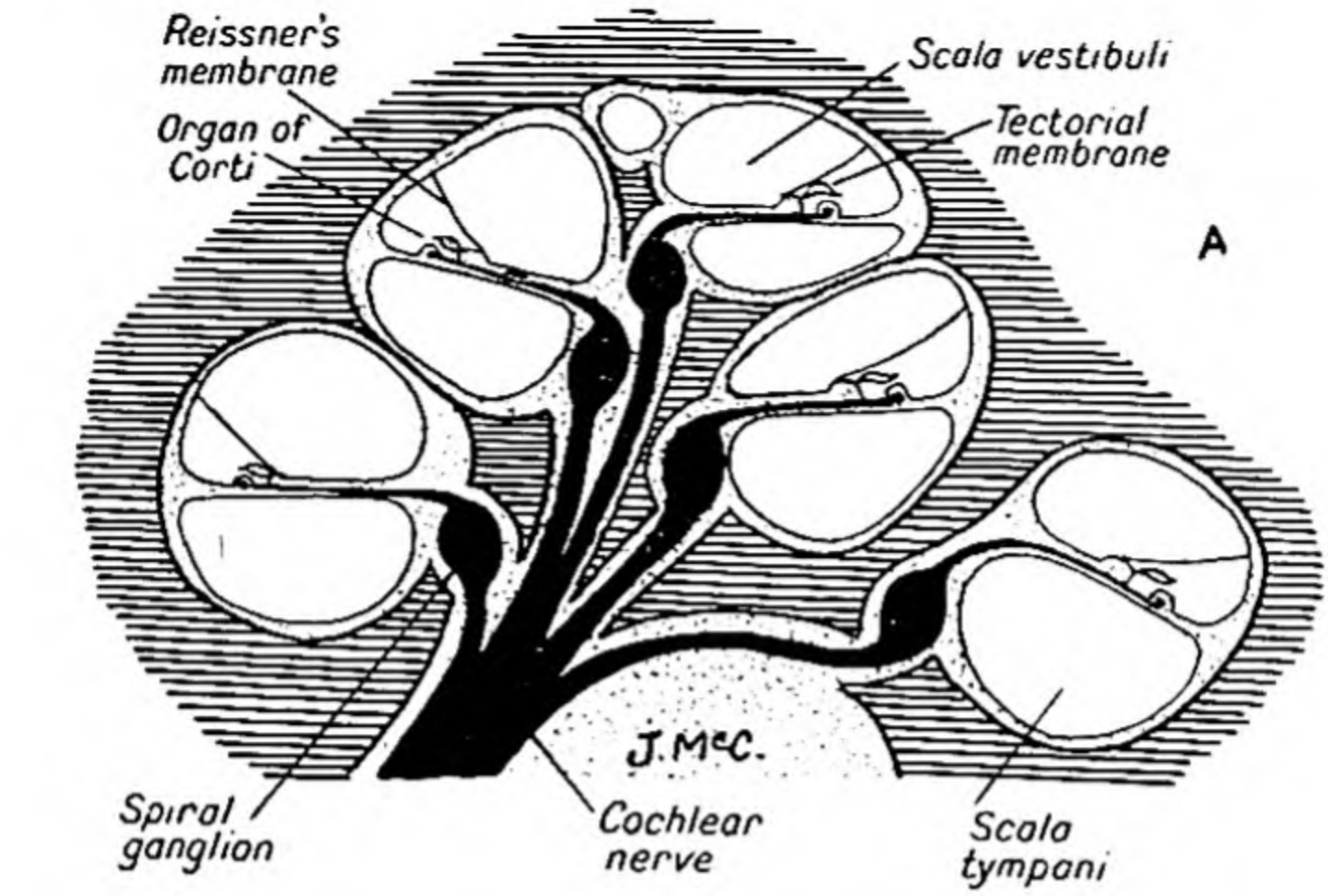


FIG. 121 – Diagram showing structure of mammalian ear. (From 'Vertebrate Zoology,' by G. R. de Beer. Sidgwick & Jackson.) *ac.*, auditory capsule; *c.*, cochlea; *de.*, ductus endolymphaticus; *Et.* Eustachian tube; *fo.*, fenestra ovalis; *fr.*, fenestra rotunda; *i.*, incus; *m.*, malleus; *oe.*, external auditory meatus (outer ear); *s.*, stapes; *sa.*, sacculus; *sc.*, semi-circular canal; *tc.*, tympanic cavity; *tm.*, tympanic membrane; *u.*, utriculus.

penetrative of coastal sea-water. The eye of the dogfish is also further adapted to function in low light intensity by the presence of a silvery layer, or *tapetum*, just behind the rods, reflecting on to the retina light which would otherwise be lost. In some dogfish this reflecting layer can



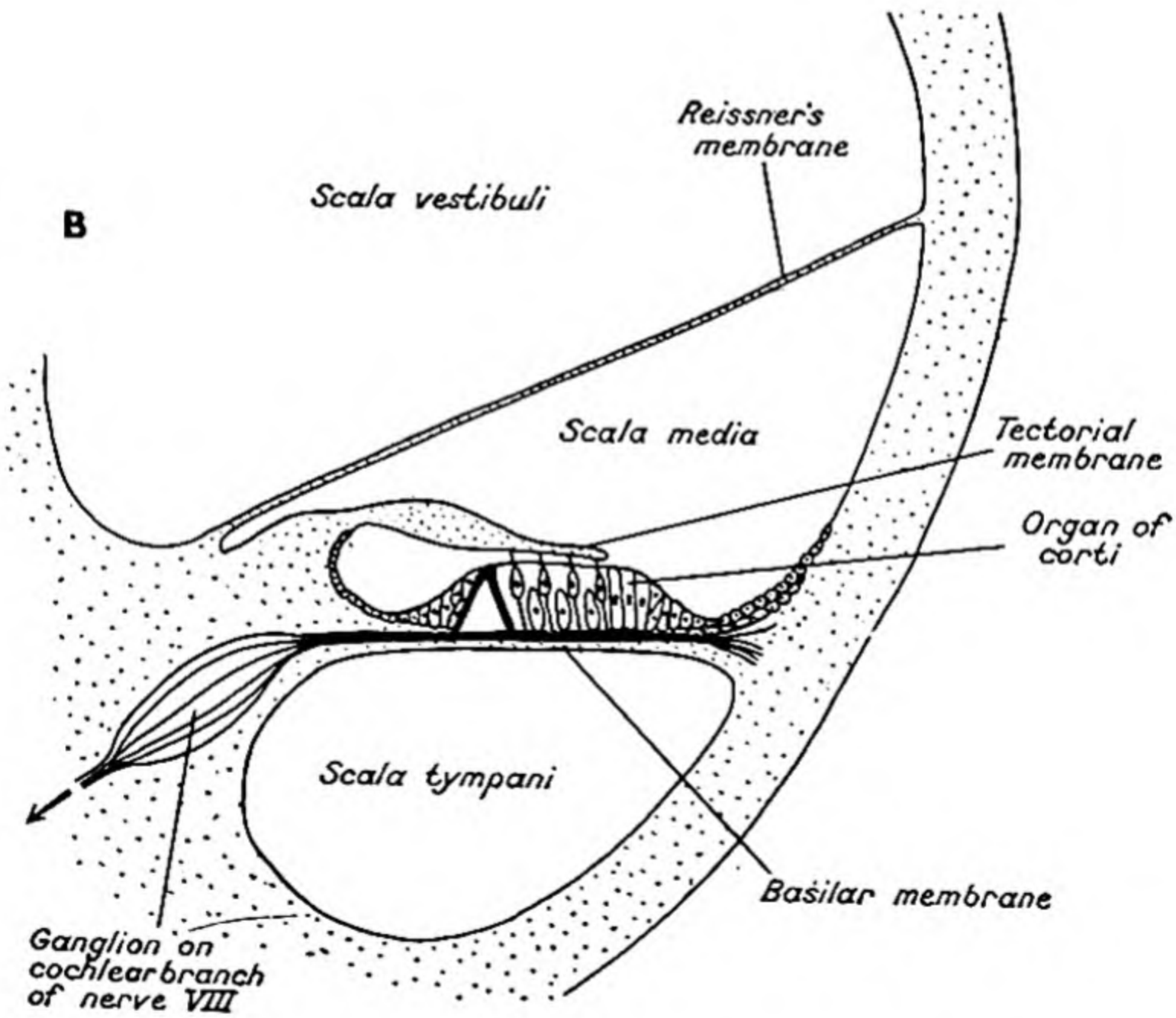


FIG. 122. The Human Cochlea, *A.*, Complete axial section; *B.*, Organ of Corti shown in greater detail.

be neutralised by the spreading across it of a dark pigment within a neighbouring layer of contractile cells, similar to the pigment cells of the skin of the frog.

(ii) *Ear*. This is fundamentally the same as that of the frog, but it differs in two important particulars. The middle ear is traversed by a chain of three ear ossicles, in place of the single columella found in the frog. But the most significant development found in the mammal is a spiral outgrowth from the sacculus, known as the **cochlea**, largely responsible for sound-discrimination. The cochlea is enclosed within a bony tube, to the wall of which it is attached at the sides. Thus in transverse section the whole structure gives the appearance of three canals, separated by membranes. The upper cavity – the **scala vestibuli** – and the lower – the **scala tympani** – are in reality spaces between the cochlear wall and its bony enclosure, whilst the centre tube – the **scala media** – is true ear cavity. The scalae tympani and vestibuli are continuous at the apex of the cochlea via a narrow tube, the **helicotrema**. The membranes separating the compartments are known respectively as **Reissner's membrane** (upper) and the **basilar membrane** (lower), though they are really the roof and floor of the cochlear tube. The epithelium of the basilar membrane becomes modified to form the **organ of Corti**. This consists of five longitudinal rows of receptor cells, interspersed with supporting cells. The sensitive cells bear processes at their free ends and are overhung by a gelatinous plate, known as the **tectorial membrane**. The basilar membrane is itself fibrous, containing the auditory strings.

The ear as a whole is vibration-sensitive. The vibrations are transmitted from the tympanum via the ossicles to the perilymph, and thence to the endolymph. Here they create disturbances in the cochlear apparatus, the impulses generated being finally conveyed to the brain in the auditory nerve. The significance of the cochlea is that it makes

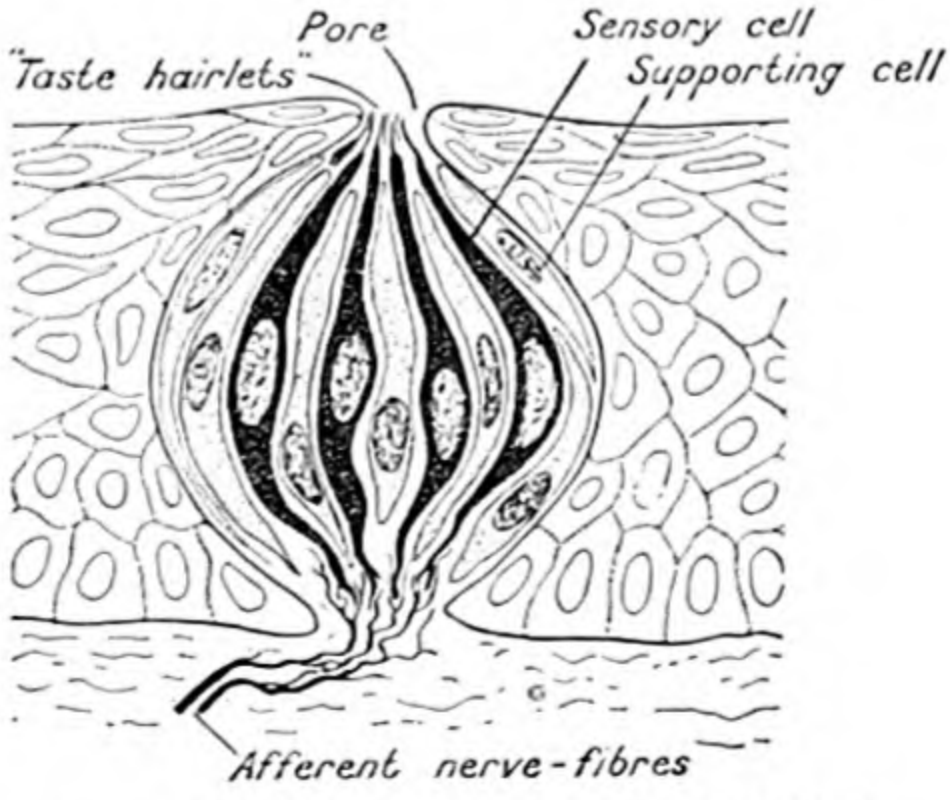


FIG. 123 – Vertical section of a taste-bud.

possible a process of sound-analysis. The remainder of the membranous labyrinth fulfils the double function of responding to the pull of gravity and twisting in space, the latter being accommodated by the semi-circular canals.

(iii) *Taste Buds.* These are chemo-receptors, occurring mainly on the tongue in mammals, but in the fish they may be found on the lips or barbels. In structure, each consists of a group of sensitive and supporting cells, contained within a pit in stratified endothelium. The sensitive cells are connected at their bases with fibres which contribute to cranial nerves VII, IX and X. In man, there are four primary sensations – sweet, sour, salt and bitter – and other flavours are merely a complex of these.

(iv) *Organs of Smell.* Each is a specialised area of endothelium (page 329) high up in the nasal cavity. Upon microscopic examination it is seen to consist of a series of columnar supporting cells, interspersed amongst which are the sensitive olfactory cells. Of these there are some fifty million in the rabbit. Each is a spherical cell, containing a nucleus. The cell itself is extended upwards to protrude slightly beyond the general surface. At its free extremity it is club-shaped and bears a number of blunt projections, each beset with very delicate cytoplasmic threads. These may serve to trap the molecules of the odoriferous substances. A second extension of the cell passes in the opposite direction to run with similar extensions of other cells as the unit components of the olfactory nerve to the fore-brain. These olfactory fibres (*i.e.* the unit components referred to above) are organised in the olfactory bulb into some two thousand streams, each ending in a so-called *glomerulus*. The impulses delivered here are conveyed mainly to a single *mitral cell*, from which they are relayed to the cerebral cortex, where final interpretation occurs.

The exact influence of odoriferous substances on the sensitive cells of the olfactory endothelium is a matter of some conjecture. It has been suggested that they initiate chemical changes in the cells, facilitated by enzymes, and that impulses are thus generated. Against such a hypothesis is the almost instantaneous perception of smells. On a physical basis a radiation theory has been advanced. The body in normal conditions emits radiations of wave-length between 4μ and 20μ. Odoriferous substances absorb radiations over a wider range than this (from 1μ to 100μ). By the absorption of infra-red radiations these particles may cause transient cooling of the endothelium, thus generating an impulse after an immeasurably small time-lag.

Coelomic Cavity

The whole of the viscera is suspended by a dorsal mesentery in a spacious coelomic cavity, or **splanchnocoel.** The posterior part, known as the **peritoneal** cavity, is separated from the anterior region by a transverse partition – the diaphragm. The anterior portion itself is further

subdivided into a **pericardial** chamber, containing the heart, and two **pleural** cavities, in each of which is lodged a lung.

Urino-genital System

As with the frog, the same organs are to some extent concerned both with excretion and with the evacuation of genital products, so that it is convenient to include them in one composite system. In both sexes the kidneys are asymmetric in position, the right one occurring some distance in front of the left. From the centre of each a ureter conveys urine back to the urinary bladder.

(A) MALE. The testes are a pair of small, rounded, oval bodies arising within the body-cavity but later passing into a pair of scrotal sacs, lateral to the penis. The path taken by each testis is indicated by a slender **spermatic cord**, composed of connective tissue and containing the spermatic

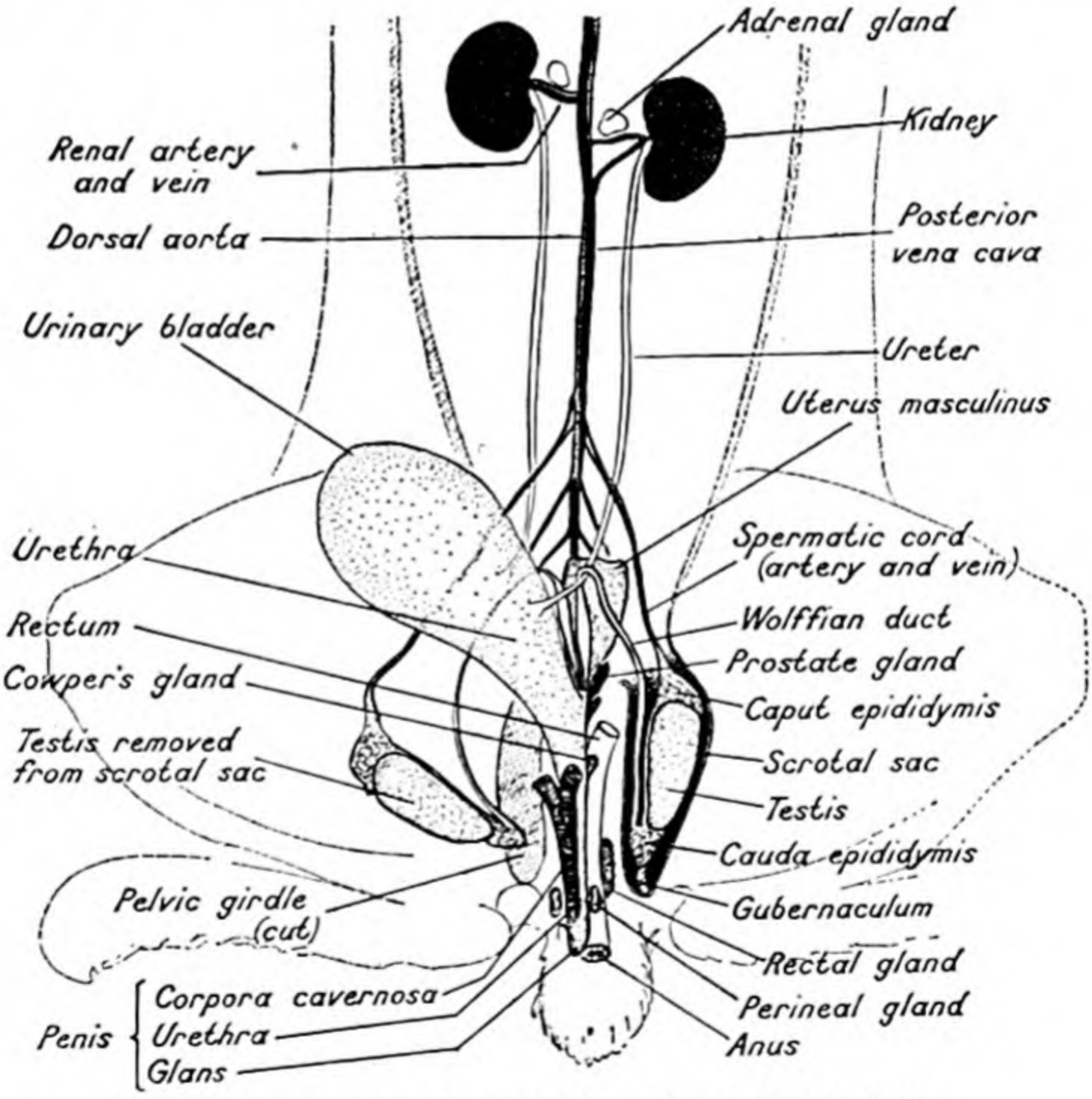


FIG. 124 – *Oryctolagus*. Male urino-genital system.

artery and vein. Each testis is partially enclosed in a mass of coiled tubes, known as the **epididymis**, connected with the wall of the scrotal sac by a band of connective tissue, known as the **gubernaculum**. From each

epididymis there passes forward a Wolffian duct, or vas deferens, which loops over the ureter to open into a median sac, representing the fused vesiculae seminales which, in most mammals, including man, are separately attached to each vas deferens, communicating with the dorsal side of the neck of the bladder. The conjoined urino-genital duct is known as the **urethra**, opening to the exterior by a muscular penis. Into either side of the fused vesiculae seminales opens anteriorly a **prostate gland** and posteriorly a **Cowper's gland.**

(B) FEMALE. In contrast to those of the frog the ovaries of the rabbit are very small, since there is little or no yolk in the eggs they produce. There is a pair of ovaries attached one behind each kidney, and every egg is enclosed in a small sac, known as a **Graafian follicle.** Near each ovary lies the opening of an oviduct. Into these an egg is discharged when

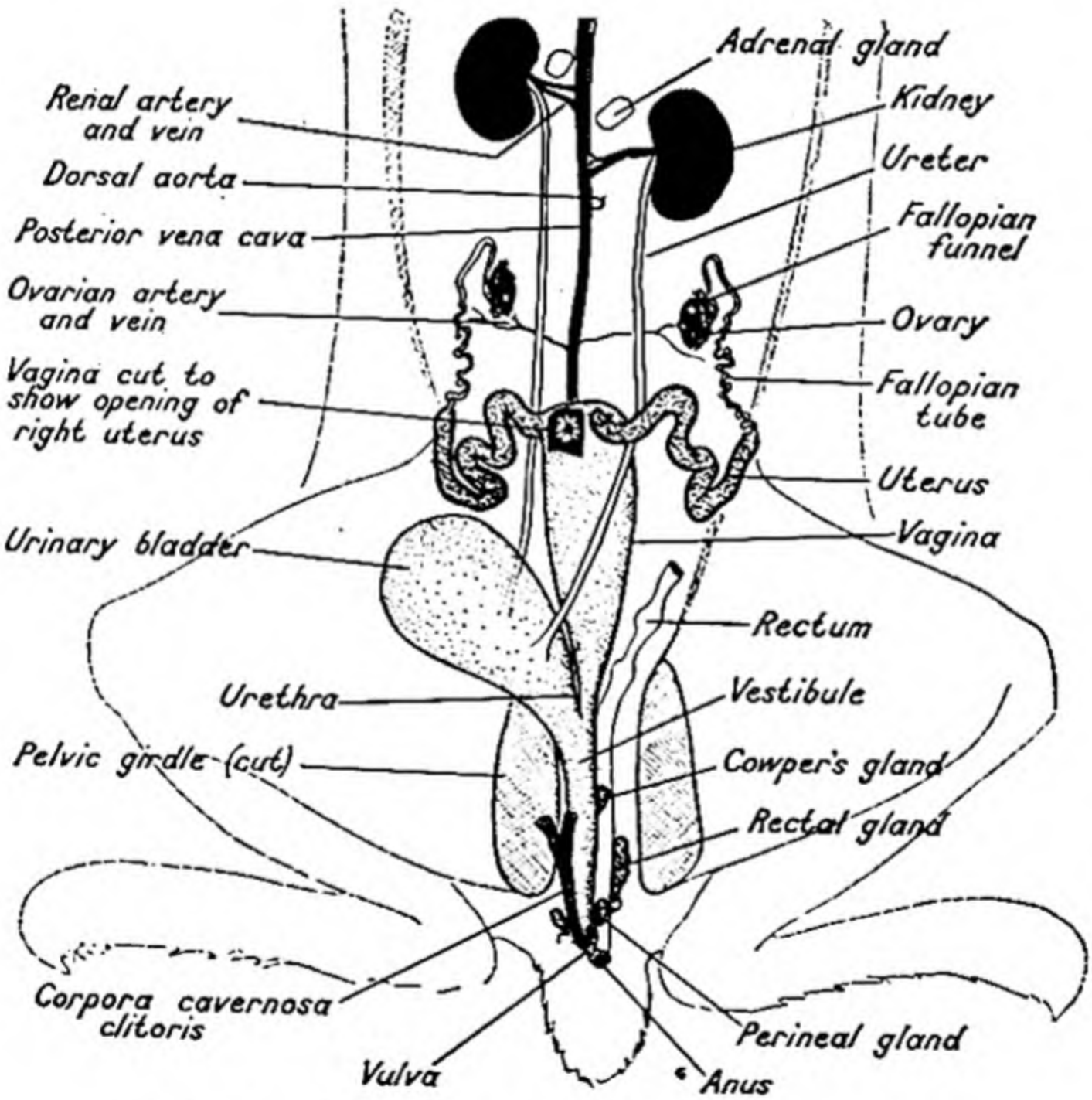


FIG. 125 – *Oryctolagus.* Female urino-genital system.

a follicle bursts. The first part of the oviduct is narrow and slightly twisted, leading into a wider, muscular part, known as the uterus, where early development of the embryos occurs. The two uteri unite to form a

median vagina, opening posteriorly into the neck of the urinary bladder to form a conjoined urino-genital duct, or **vestibule**, which communicates with the exterior by the vulva. On the ventral wall of the vestibule lies a rod-like **clitoris**, representing the penis of the male, whilst dorsally there occurs a pair of small Cowper's glands.

(C) REPRODUCTION. Breeding occurs mainly between January and June. At this time there is a periodic ripening of eggs. When ripe they are shed into the oviducal funnels and clump together at the top of the Fallopian tube. This phenomenon is known as **ovulation**, taking place spontaneously when copulation (coition) occurs. In this event sperms are injected into the body of the female by the male, the penis becoming erected by an increase of blood-pressure, and being then inserted into the vulva. The sperms pass up the vestibule in the fluid lining its wall, and one eventually fuses with each ovum present. Development then takes place within the uteri, each embryo becoming attached by a stalk, or **umbilical cord**, which penetrates a specialised zone of the uterine wall, termed the **placenta**. Here intimate contact (but *not* union) is achieved between capillaries of mother and offspring, so that food and oxygen may be exchanged for waste matter, including carbon dioxide. This is fully described on page 544. Many members of larger litters are completely resorbed into the wall of the uterus. After rather less than a month development is completed, this interval being known as the period of **gestation**. The process of **parturition** then occurs, the young rabbits (usually four or five) being forced to the exterior through the vulva by the contraction of the walls of the uteri and vestibule. This type of reproduction, wherein the young are retained within the body of the mother, is described as **viviparous**, as compared with the oviparous form like that in the frog, involving the laying of eggs and their subsequent development in the outside world. In the case of mammals the young, even after birth, are nourished on a milky secretion produced in the mammary glands of the mother. Prior to the birth of her offspring the mother prepares a nest of leaves and fur within the burrow.

Endocrine Organs

The principal endocrine organs are the thyroid, parathyroid, thymus, pituitary and adrenal. The **thyroid** is a bi-lobed structure, contained in a fibrous capsule and lying immediately posterior to the larynx, with the main masses situated one on either side of the trachea and connected ventrally. The **parathyroids** are embedded within the thyroid, whilst the **pituitary** occurs beneath the floor of the mesencephalon, lying in a depression in the floor of the skull, known as the **sella turcica**. The **islets of Langerhans** are microscopic patches of tissue embedded in the pancreas, whilst anterior to each kidney is a small **adrenal body**. The **gonads**, too, as well as elaborating genital products, act as endocrine organs, as discussed in Chapter 27. In the pregnant female the burst Graafian

follicle becomes an endocrine organ, known as the **corpus luteum**, responsible for certain somatic changes accompanying pregnancy.

PRACTICAL WORK

Dissect a rabbit after examination of its external characters. The dissections are best done in the order alimentary (abdominal portion), urino-genital and vascular systems, followed by a careful investigation of the structure of the neck. In the second dissection the vascular system and neck should be attempted first while the animal is still fresh.

Study the articulated skeleton, noticing the relative positions of the bones. Afterwards draw and label fully the separate bones, including a representative of each region of the vertebral column, together with both the atlas and the axis.

Study carefully the skull of the dog, identifying the individual bones and foramina, for which the tables on page 150 may prove of assistance. Draw lateral, dorsal and ventral views. (The skull of a young dog is preferable, since the sutures are more readily discerned.)

PART II

Plant Anatomy

This is intended to form a complement to Part I, for selected types are described, with principal emphasis on their anatomy, though this is to some extent related to the performance of life-processes. Especially is this so in connexion with the simpler plants, where the processes of reproduction and sexual fusion should be carefully studied, as well as in the life-histories of *Pinus* and Angiospermae in their relation to cones and flowers respectively. But in the main a consideration of physiological processes is reserved for Part III.

CHAPTER 9

Selected Algae

The members of the plant kingdom are classified primarily according to complexity of structure. The lowest forms are not divisible into root and shoot, nor have they any well-defined conducting tubes for their food materials. Together they comprise the group known as the **Thallophyta**, important amongst which are the Algae, characterised by the presence of chlorophyll, as well as by the simplicity of structure significant of the Thallophyta in general. Their structure may best be understood by the study of a number of individual types.

I. CHLAMYDOMONAS

Structure

Chlamydomonas is a minute, non-cellular (Chapter 21) organism, occurring on the surface of stagnant ponds and, with other related plants, responsible for the characteristic green colour. Each individual is only one-fiftieth of a millimetre in diameter, and is approximately spherical in shape. It is bounded by a thin wall of cellulose, produced into a papilla

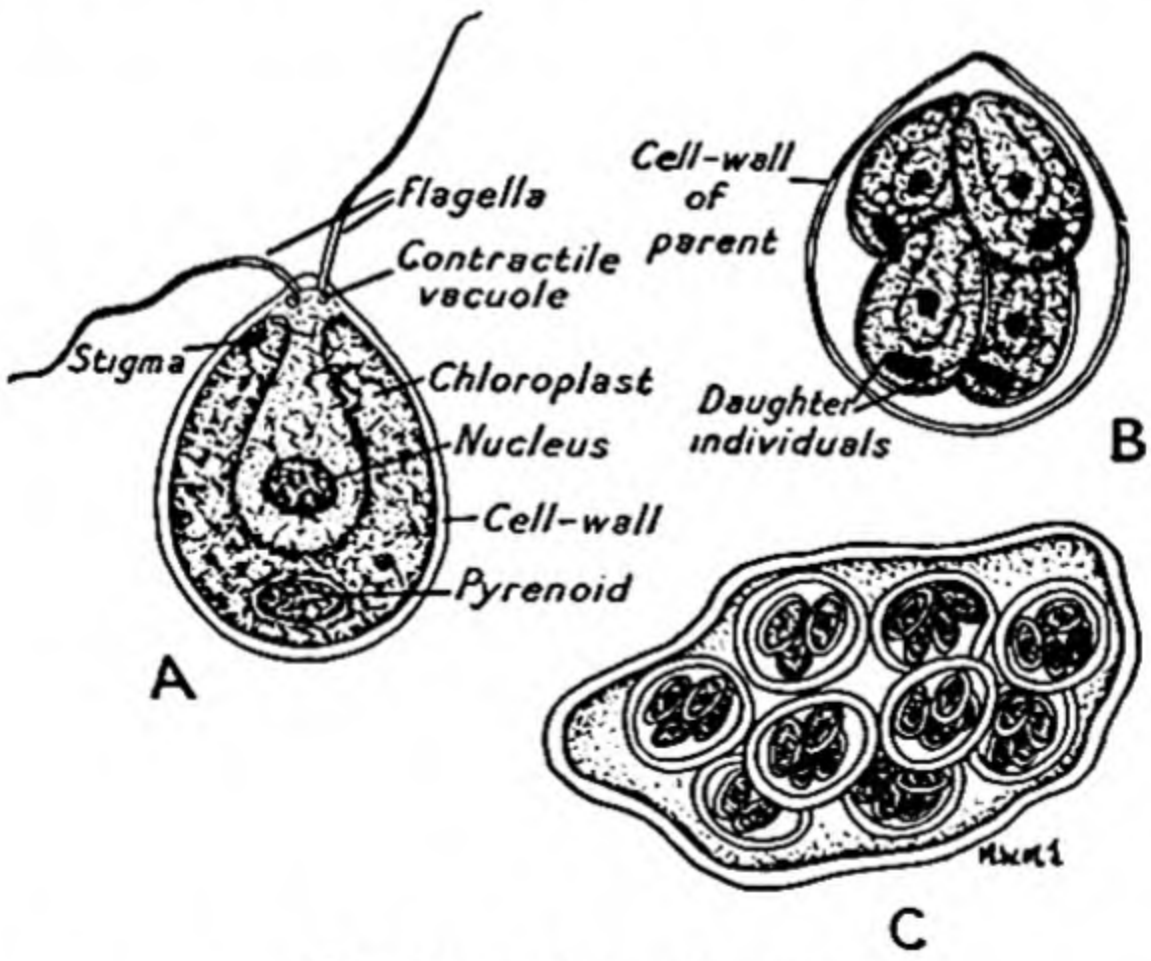


FIG. 126 – *Chlamydomonas*.
A, A single individual; *B*, Asexual reproduction within the cell-wall of the parent; *C*, Palmelloid stage.

at the anterior end. The bulk of the cavity enclosed by this wall is occupied by a large **chloroplast**. This is a cup-shaped structure, with its concavity directed forwards. It is very much thickened at the base, and throughout is distributed **chlorophyll**, the characteristic pigment of green plants. Embedded in the base is a structure known as a **pyrenoid** – a colourless region associated with the formation of starch. The remainder of the cavity is filled with protoplasm, which itself may contain numerous **starch grains**. Near the margin of the chloroplast on one side lies a small, light-sensitive eye-spot, or **stigma**, responsible for the movements of this organism in response to intensity and direction of light. In a comparatively clear region at the anterior end lies a **nucleus**, suspended by protoplasmic threads. In front of the nucleus, in a clear region of the cytoplasm, there are two small **vacuoles**, which contract at intervals, like those of *Amoeba* and *Paramecium*. They may possibly serve for the elimination of excess water. Two delicate, protoplasmic processes project from the anterior end. Each is a **flagellum**, and by their combined backward movements the organism is drawn forward, the motion being accompanied by a rotation about the long axis. It is on account of the direction of movement that the end bearing the flagella is designated as anterior.

Life-processes

Chlamydomonas and some of its allies are peculiar amongst plants in that they are motile, locomotion being effected by means of the flagella. As detailed in Chapter 26 the movements of these plants are not without reference to external conditions, and the influence of light is particularly important in this respect. But, as in other green plants, nutrition in *Chlamydomonas* depends on photosynthesis, a process fully described in Chapter 23. Water and dissolved mineral salts enter the organism through their permeable walls in a manner similar to that responsible for their absorption from the soil by the root-hairs of higher plants. But whereas terrestrial plants absorb carbon dioxide in gaseous form, this essential food must be absorbed in aqueous solution by all aquatic plants. In like manner the oxygen necessary for respiration enters the plant in solution in the water.

Life-history

In favourable conditions *Chlamydomonas* reproduces in much the same manner as *Amoeba* – by binary fission. When an organism has attained by growth its definite adult size it comes to rest, withdrawing its flagella. The contents become slightly withdrawn from the wall, and very soon the nucleus is seen to be dividing into two equal halves. When this process is completed, it is followed by a constriction of the cytoplasm in such a way that each half of the cytoplasm contains a daughter nucleus. Each of the daughter individuals thus formed may divide again in a

similar manner, and this may be followed by a third division, resulting in the formation of eight small cells. At this stage the parent cell-wall bursts, thus liberating the products of division, each of which has by now formed a wall of its own, and thus resembles the parent in everything but size, since new flagella and vacuoles have been developed. Under suitable circumstances this process may be repeated every twenty-four hours, so that by the end of a week some two million individuals may have been produced. Such reproduction, effected merely by fission and not involving any form of fusion, is described as asexual.

When conditions are less favourable, though not particularly severe, the daughter cells may be retained within the cell-wall of the parent, the wall itself becoming mucilaginous. The daughter individuals continue to grow, and eventually they themselves divide, whilst at this stage their

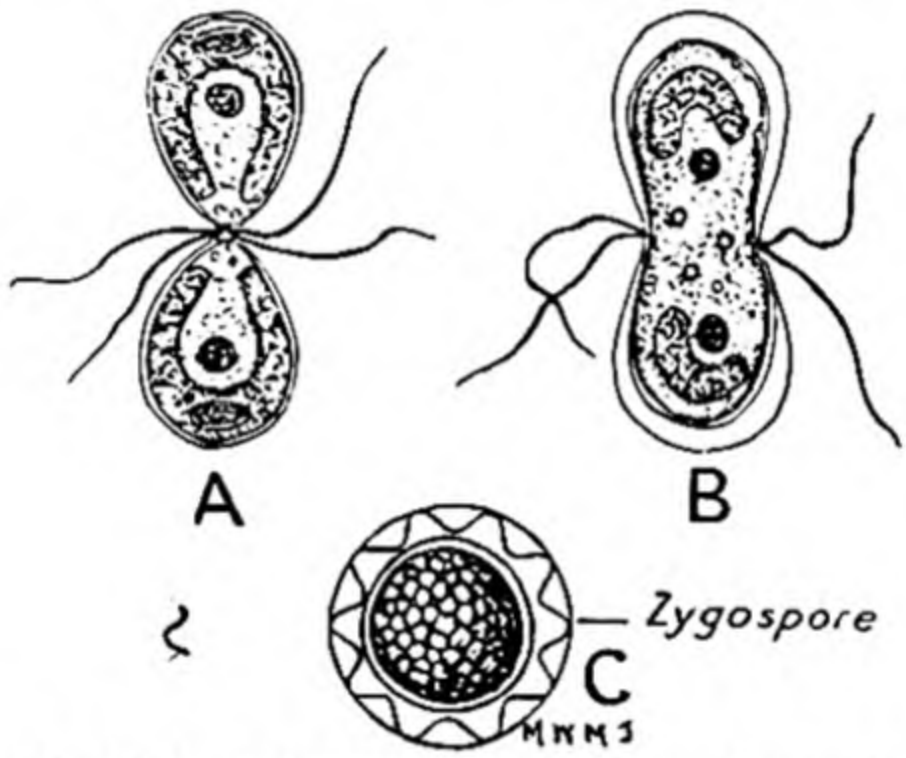


FIG. 127 – *Chlamydomonas*. Stages in sexual reproduction.

own walls become mucilaginous. It is possible, depending on conditions, for this process to be repeated several times, resulting in the formation of a series of mucilaginous capsules, arranged in groups in larger capsules. Such a composite body constitutes what is known as a **palmelloid stage** in the life-history of *Chlamydomonas*. When conditions again become favourable the ultimate products of division are liberated, each becoming a normal adult.

A final phase in the life-history appears only when active growth is prevented, usually by the advent of really adverse conditions. It commences by a form of division similar to that responsible for asexual reproduction, but distinguishable from it by the formation of more products, some sixteen or thirty-two daughter cells being formed. These are known as **gametes**, being considerably smaller than ordinary individuals and frequently devoid of a cell-wall. They fuse in pairs, and most important in the process is the complete coalescence of the two nuclei. The resultant body is termed a **zygote**, and at first possesses four

flagella, by means of which it moves about for a short period. Eventually it comes to rest, withdrawing its flagella and secreting about itself a hard, thickened coat. Within the cytoplasm may be observed droplets of a red, oily liquid, possibly a food-reserve. In this condition it is known as a **zygospore**, and may resist severe degrees of adversity, including desiccation and low temperature. Zygospores are distributed by wind, and eventually, when a suitable environment is discovered, division occurs within the thick wall. Finally the products are liberated to grow into adult plants.

2. HAEMATOCOCCUS

In many respects *Haematococcus* resembles *Chlamydomonas*, and it is necessary therefore only to note the points of difference. The living contents of the cell are separated from the bounding wall by a wide layer of mucilage, traversed by protoplasmic threads. The chloroplast is not

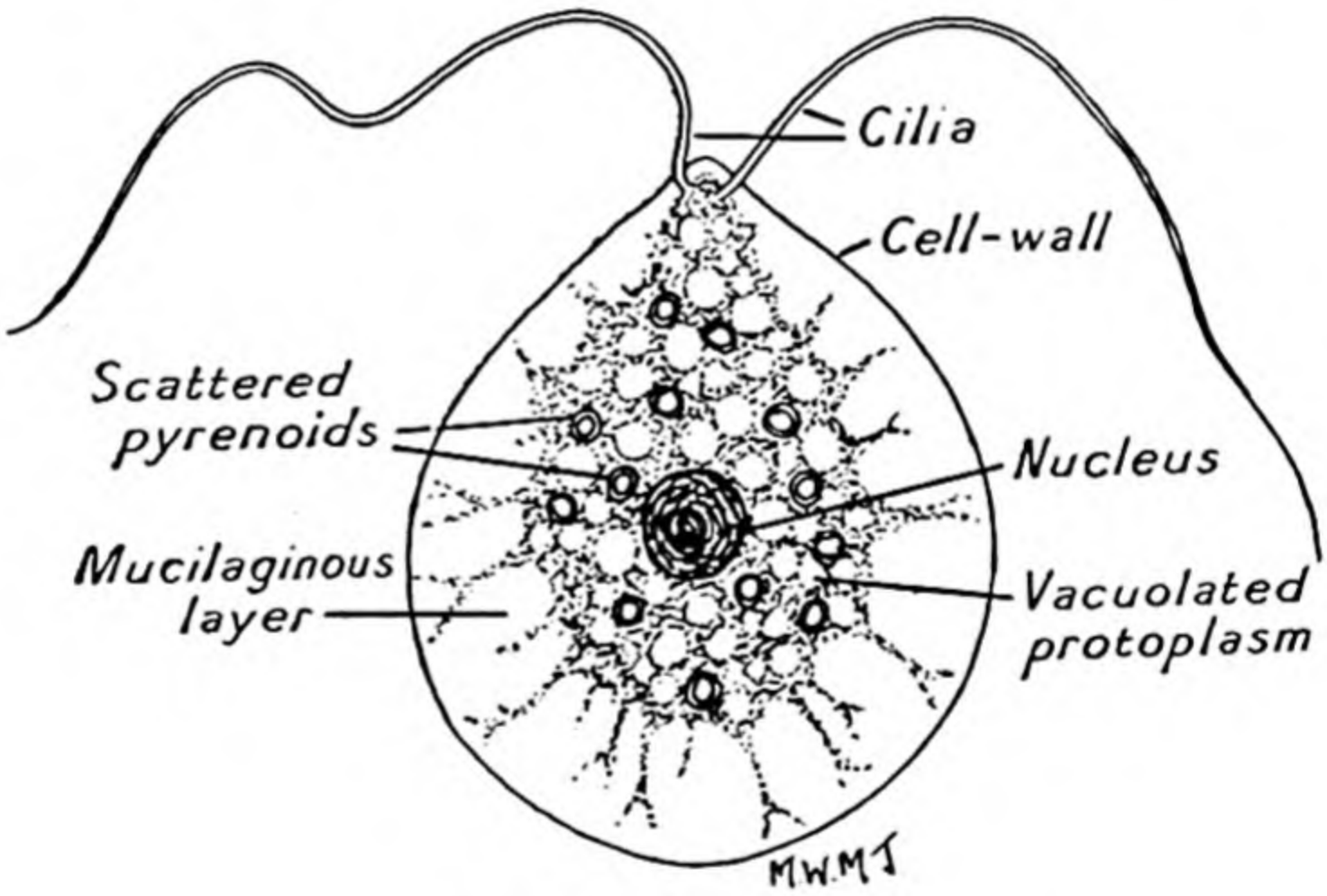


FIG. 128 – *Haematococcus*.

well defined, though it occupies the marginal region of the protoplast (living contents, as distinct from cell-wall and mucilage). Pyrenoids are distributed throughout the chloroplast, whilst the vacuoles are numerous and scattered freely in the protoplast. A red pigment (hence the name of the genus) frequently appears in the cytoplasm, imparting a characteristic colour to the water or mud on which the plant is growing.

3. PLEUROCOCCUS

Pleurococcus, known also as *Protococcus*, differs from *Chlamydomonas* in one very important respect, namely, that it is sessile, having no flagella. Further, whereas *Chlamydomonas* is aquatic, *Pleurococcus* occurs on the trunks of trees and wooden railings in the form of a green, powdery

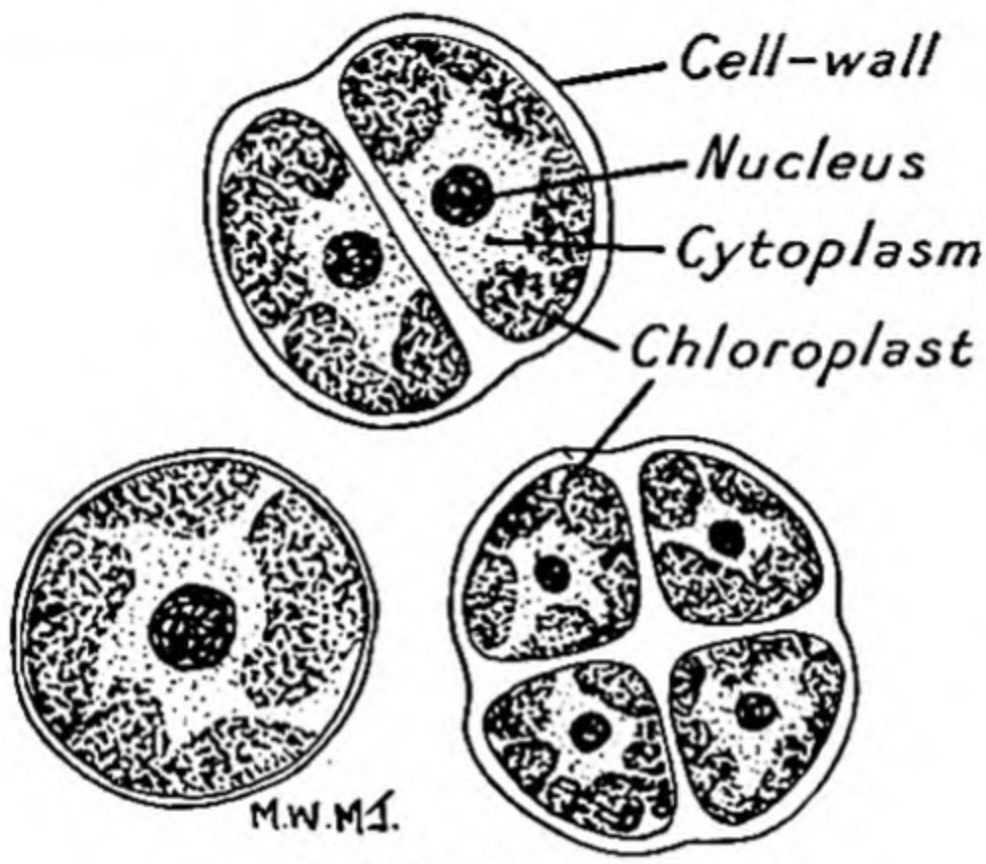


FIG. 129 – *Pleurococcus.*

covering. The cell-wall is thick, whilst the chloroplast is divided into a number of lobes. The cells exist normally in groups of four, formed by division of a single parent cell. In moist situations short filaments are sometimes produced, showing a simple type of branching. Actually the ordinary vegetative cells of *Pleurococcus* are so resistant that they are regarded by some authorities as comparable with the zygospores of other Algae.

4. VOLVOX

Structure

This plant differs from those previously described in that it consists, not of a single cell, but of between 200 and 25,000 essentially similar cells associated together to form what is generally referred to as a colony (see page 352). Each cell resembles *Chlamydomonas* except in that its cell-wall is thick and mucilaginous, being traversed by numerous protoplasmic processes, which are continuous between component cells of the colony. In *V. aureus* these processes are delicate, whilst in the *globator* species they are much stouter. Each cell contains a chloroplast, a nucleus, a stigma and a pair of flagella, the last-named being directed outwards

from the surface of the colony, which is thus rendered motile. All the cells are embedded in the wall of a hollow, mucilaginous sphere, which communicates with the exterior by a minute pore. The cavity of the sphere contains a watery fluid.

The colony as a whole consists of four types of cell. The vegetative

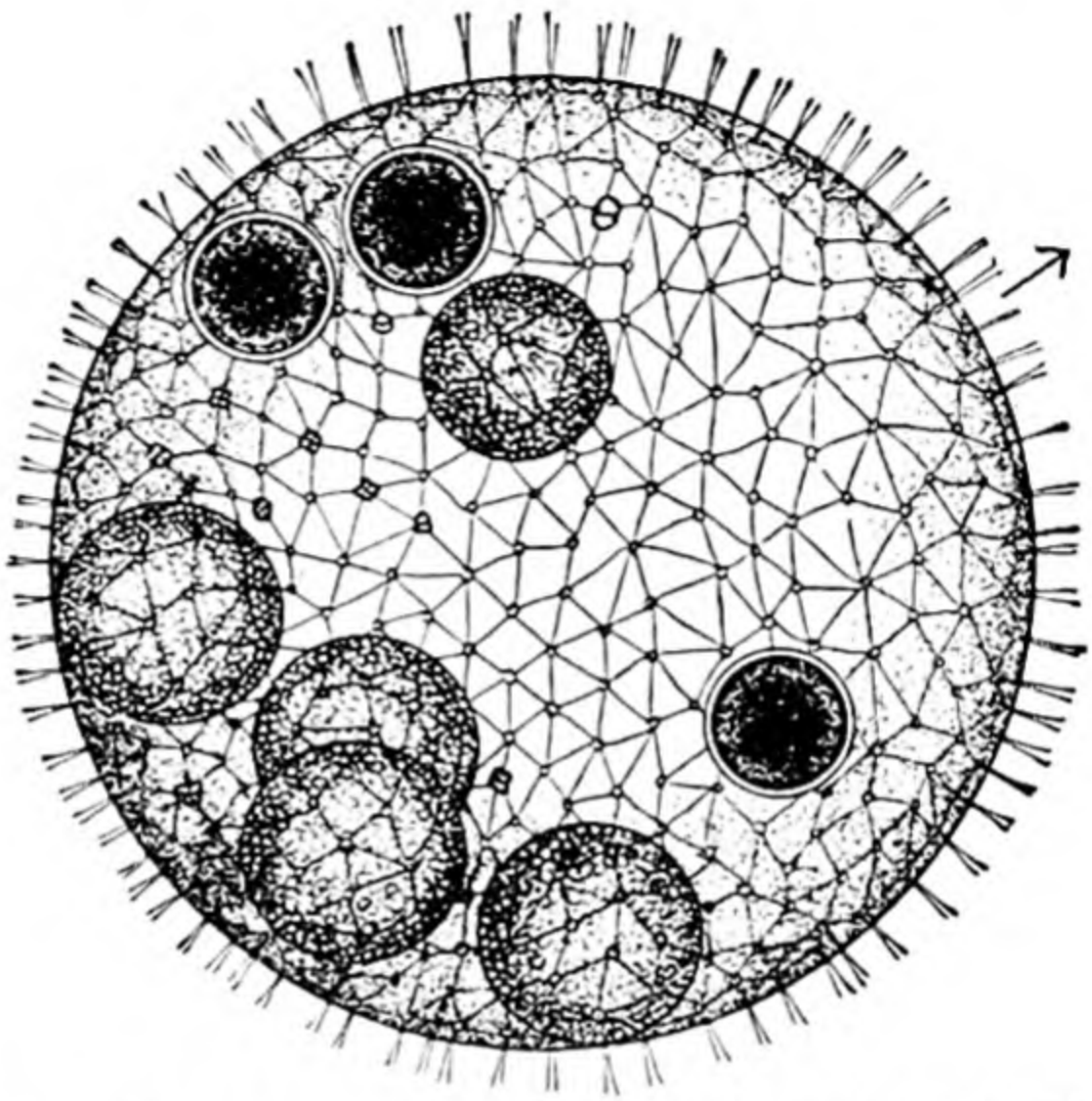


FIG. 130 – *Volvox aureus*. X 180. (From 'Elements of Plant Biology', by A. G. Tansley and W. O. James. George Allen & Unwin.)
A coenobium which has produced all three kinds of germ-cells. The three large (walled) spherical cells are fertilised eggs, the small groups of cells are derived from antheridia, which will divide further to form sperms, the largest spheres are young coenobia derived from spores; division in these last is complete, but the cells have not yet separated. Note that about a quarter of the mother coenobium (the front quarter) is free from reproductive cells. The arrow shows the direction of locomotion. (After Klein.)

cells are by far the most numerous, and are responsible for nutrition and locomotion of the colony. The three remaining types are all concerned with reproduction, and comprise about 1% of the total number. They will be described in the following paragraph.

Reproduction

Multiplication is effected by both asexual and sexual means.

Asexual. The mother-cells from which daughter colonies are formed are distinguishable from the vegetative cells by their greater size. They divide rapidly, and the products of their division become disposed in the

shape of a new *Volvox* colony, projecting into the cavity of the parent, from which they are eventually liberated when the latter fragments. A further generation may arise in a similar manner within the daughter colonies before liberation takes place.

Sexual. This involves the presence of the remaining two types of cell, known as **oögonia** and **antheridia**. Each oögonium is relatively large, dark green in colour and non-flagellate. It absorbs nourishment from surrounding cells and eventually becomes an egg-cell.

An antheridium divides to form either 32 (*aureus* species) or 128 (*globator* species) cells. These become spermatozoids. In the *aureus* species each is green and has two minute flagella attached at one end, whereas in the *globator* species each is yellow and the flagella are attached in the middle. These spermatozoids are eventually set free into the cavity of the parent colony. They subsequently fertilise egg-cells of either the same or a different colony, the latter event involving their previous escape from the parent via the pore.

Following the fertilisation the zygote becomes dark in colour and thick-walled. It germinates only after being liberated by the breaking up of the parent colony.

It is not certainly established whether or not all three types of reproductive cell can be present in the same colony, but it is known that in the *globator* species antheridia and oögonia can occur together, whereas in *V. aureus* they are found in separate colonies.

5. SPIROGYRA

Structure

Spirogyra is an Alga of a rather different type. It is filamentous, each filament consisting of a number of cylindrical cells, placed end to end. The plant is aquatic, occurring abundantly entangled in water-weeds at the bottom of stagnant ponds or in floating masses on the surface. Each cell is bounded by a **cell-wall**, lined with a thin layer of **cytoplasm** and covered externally with a film of mucilage. The bulk of the cavity of the cell is occupied by a large **vacuole**, in the centre of which is suspended a conspicuous **nucleus** by means of delicate protoplasmic threads. The **chloroplast** takes the form of a spiral band, lying in the protoplasmic lining and running throughout the length of the cell. At intervals along the chloroplast are colourless patches – the **pyrenoids** (see page 182).

Life-history

Reproduction is effected by transverse division of the cells, thus effecting increase in length of the filament as each daughter cell grows to the size of the parent. Occasionally a thread may fragment, after which each portion continues to grow in length, thus accommodating an increase in the number of threads.

CONJUGATION. When conditions are unfavourable to continued asexual reproduction gametes are formed, though their form and behaviour differ from those of types previously described. Two threads lying side by side make random contact and subsequently give rise to gametes at intervals throughout their length, and the behaviour of two opposite filaments (Fig. 132, *A* and *B*) will be considered. From one of the cells of filament *A* a projection is put out from the cell-wall in the direction of the cell lying alongside it (Fig. 132, cell 1). This is followed by a similar process in filament *B*. Very soon the processes meet (Fig. 132, cells 2), and eventually open communication is established (Fig. 132, cells 3). In the meantime the protoplasmic contents of the cells concerned have become condensed to form a compact mass, this process occurring slightly earlier in the cell of filament *A* than of filament *B* (Fig. 132, cells 1, 2 and 3). The contents of the cell of filament *A* now pass across the **conjugation canal**, as the connecting tube is termed (Fig. 132, cells 4). Within the corresponding cell of filament *B* fusion of the two lots of cell-contents occurs, including complete coalescence of the two nuclei (Fig. 132, cells 5), so that a zygote is formed. The wall of the zygote becomes thickened, eventually constituting a **zygospore**. In one filament (*A*) there will now be a large number of completely empty cells, whilst filament *B* will give rise to a corresponding number of zygospores, for it must be remembered that a large number of pairs of cells of the two filaments complete this process of conjugation more or less simultaneously, though for convenience they have been shown in Fig. 132 as if at successive stages throughout the length of the filament. The filament which has lost most of its contents perishes, whilst of the other filament only the zygospores survive. These eventually germinate, the outer coat bursting and the contents growing out to form first a new cell, and ultimately a new filament. The reduction in chromosome-number (see page 316) is effected in the first two divisions of the zygote, so that all the cells of the filament are haploid. In one species of *Spirogyra*

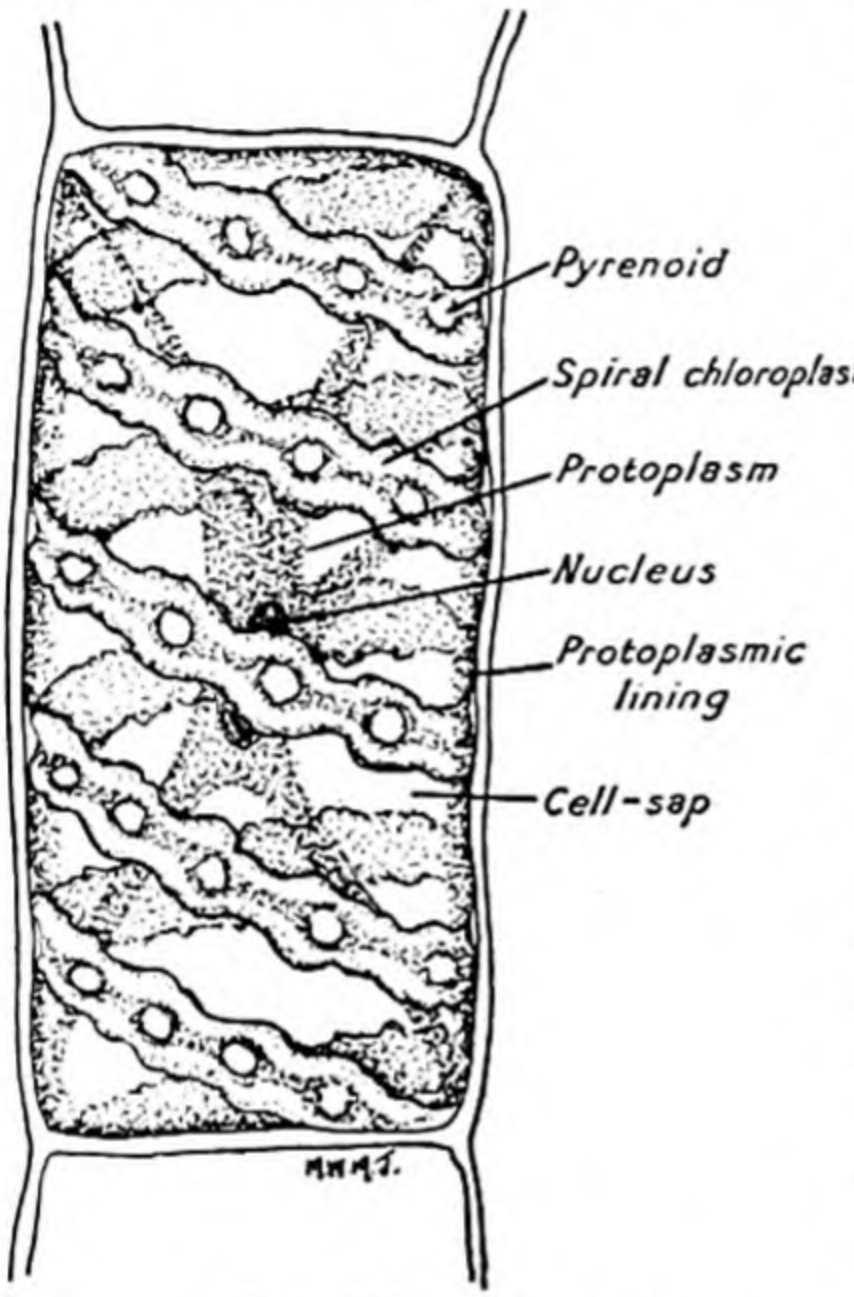


FIG. 131 – *Spirogyra.*

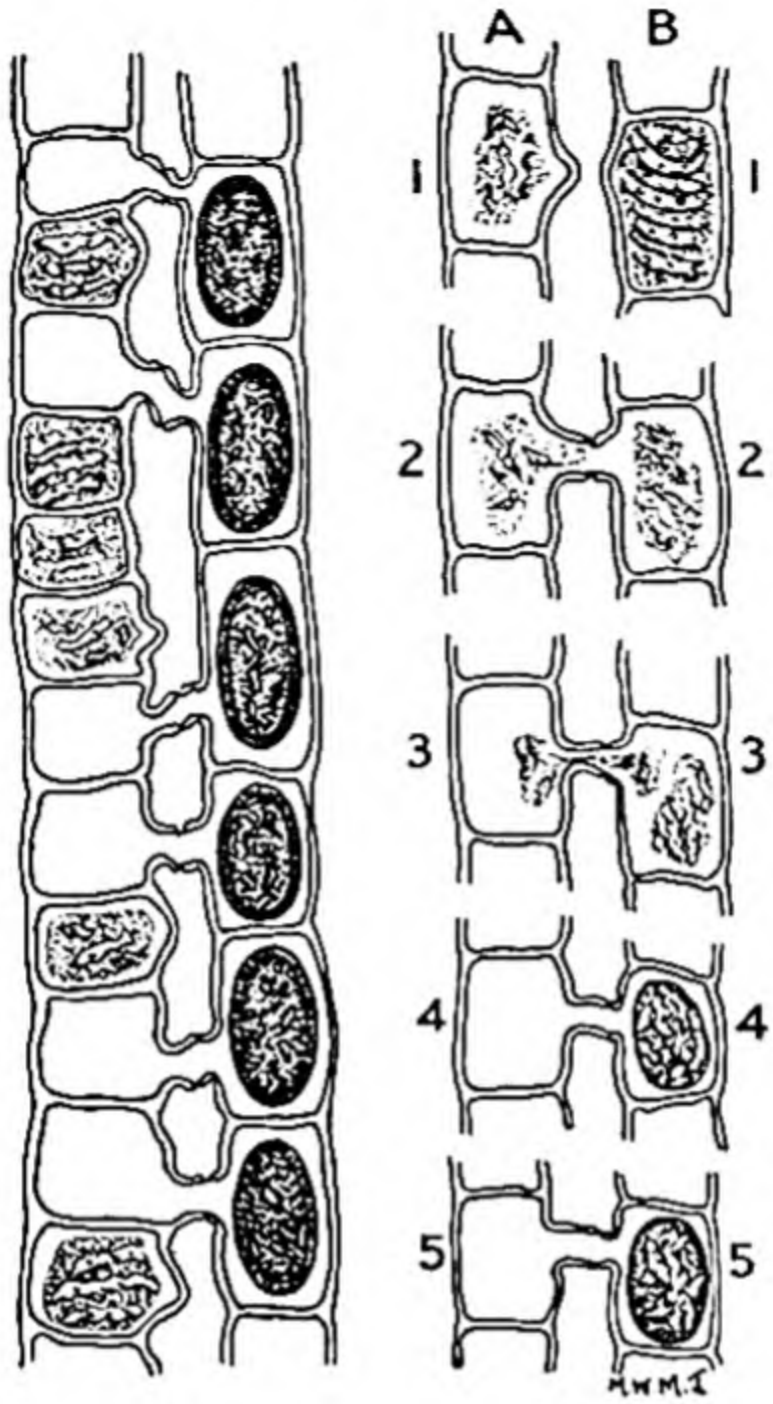


FIG. 132 – *Spirogyra*. Stages in conjugation.
For description see text.

both filaments are at the same stage throughout, so that the gametes fuse in the conjugation canal.

6. VAUCHERIA

Vaucheria is an Alga exhibiting a somewhat more advanced degree of organisation, especially in the matter of specialisation for conjugation, than is found in *Spirogyra*.

Structure

Vaucheria is a filamentous Alga, occurring commonly in fresh water or on damp soil. The separate filaments are branched, and are non-septate. As each contains several **nuclei**, the filaments are described as coenocytic (page 308). Transverse walls in Algae such as *Spirogyra* are important in affording mechanical support. In *Vaucheria* this is provided almost entirely by the turgor (page 378) of the filaments, with the result

that they very readily collapse after injury. Each filament contains, as well as many nuclei, a large number of small, discoid **chloroplasts**, whilst some of the branches, termed **rhizoids**, are colourless, and effect attachment to the substratum. The chloroplasts contain no pyrenoids, and excess food is stored as oil.

Life-history

Vaucheria reproduces asexually by means of **swarm spores**. The contents of a hypha become much condensed in a swollen tip, which is then

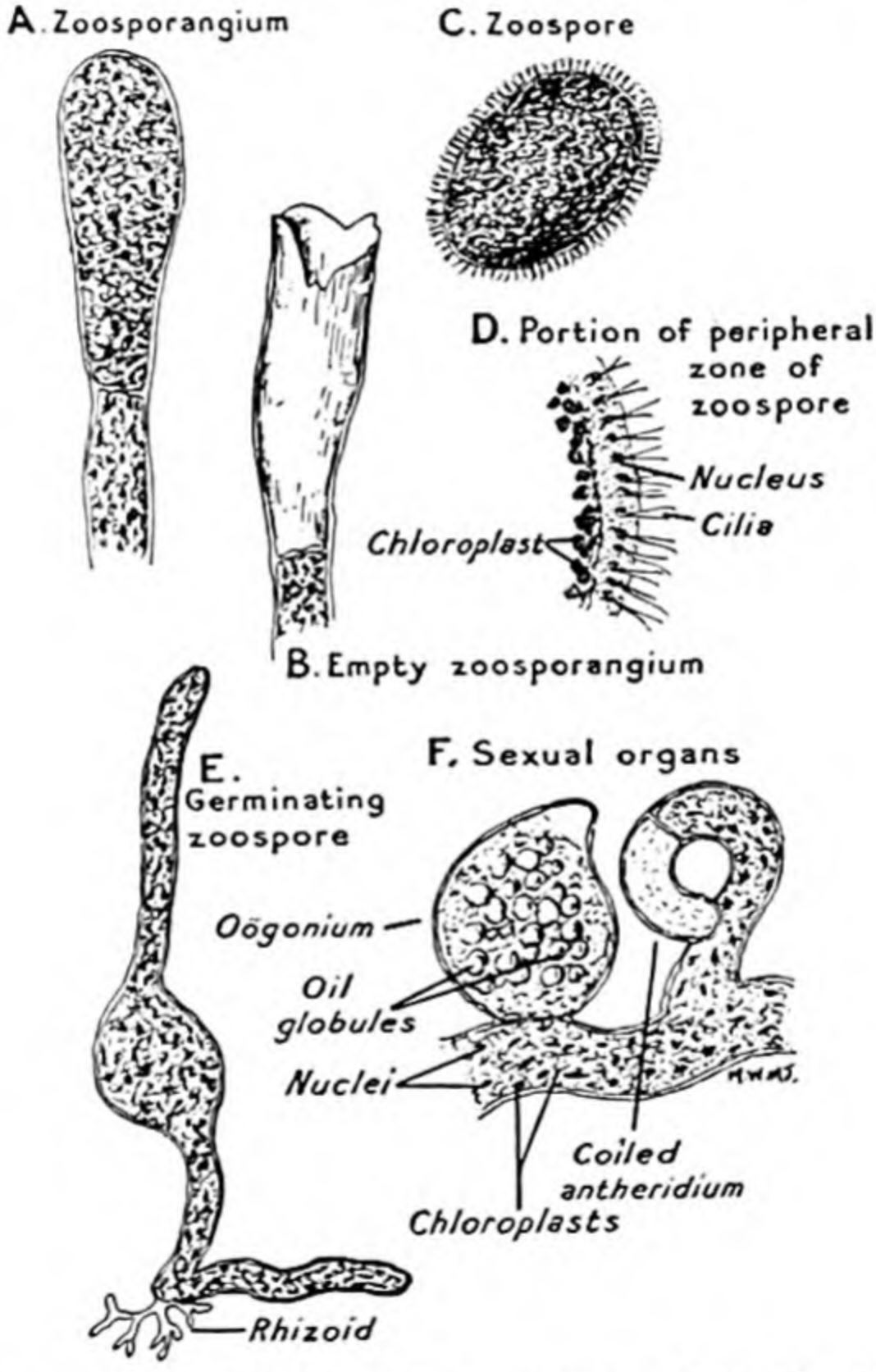


FIG. 133 – *Vaucheria*. A-E Formation, and germination of zoospore; F, Sexual organs.

cut off from the remainder by means of a transverse septum. This body constitutes a **sporangium**, and its entire contents become converted into a single large, green swarm spore. It escapes with the rupture of the end

wall of the sporangium, rotating about its longitudinal axis during its passages to the exterior. It is a multi-nucleate body, the nuclei lying in a clear layer of peripheral cytoplasm, whilst pairs of cilia, corresponding in numbers and position to the nuclei, project from its surface. The whole swarm spore corresponds to the total number of separate zoospores produced by many other Algae. The whole body is by some authors termed a zoospore. After a short period of activity a thin wall is formed, and the swarm spore elongates, one of the two ends becoming attached to the substratum by a rhizoid.

Conjugation is effected by means of specialised structures, termed oögonia and antheridia. These arise at the tips of branches, either main or lateral, and are cut off by transverse partitions from the remainder of the filament. The protuberance destined to become an **oögonium** is at first multi-nucleate, but all the nuclei save one – that of the future egg-cell – recede into the base of the filament prior to the formation of the transverse septum. On one side of the mature oögonium is a beak-like projection, at the end of which open communication with the exterior is soon established. The **oösphere**, or egg-cell, then rounds itself off, and is enclosed in a mass of colourless protoplasm. Self-fertilisation is probably the rule, since an **antheridium** normally matures in the near neighbourhood of an oögonium. Each antheridium is a coiled tube, within which are formed many minute, pear-shaped **spermatozoids**, each with a pair of cilia on one side. These spermatozoids escape from the antheridium by the rupture of the end wall of the latter, and are chemotactically (page 454) attracted to the egg-cell as a result of the exudation of mucilage by that body. Fertilisation results in the conversion of the oösphere into an **oöspore**, which soon becomes enclosed within a resistant wall, whilst stores of oil are accumulated. Following the resting period which ensues, a new plant arises by direct development on germination of the oöspore.

PRACTICAL WORK

Chlamydomonas, *Haematococcus*, *Pleurococcus* and *Spirogyra* should be obtained fresh. Examine each successively under low and high power and with oil-immersion, noting progressively finer details of structure. Stain with iodine and re-examine with a view to discerning starch grains, and flagella in the motile forms. In *Spirogyra* look for stages in conjugation. If these cannot be discovered in fresh specimens examine a prepared slide. Make drawings to illustrate the detailed structure of each type.

Examine complete coenobia of *Volvox* under low power, noting the distribution of various kinds of cell, and perhaps the presence of daughter-colonies within the parent. Examine individual cells under high power and with oil-immersion. If obtainable, stain *Volvox* with dilute methylene blue to see the lamellae between neighbouring cells.

CHAPTER 10

Fucus

Fucus, a further representative of the Algae, differs from forms previously described in that it exhibits a certain degree of specialisation, or differentiation, and in this respect shows a considerable advance over the simpler types. This differentiation assumes two forms:

(i) The body is divisible into three distinct regions, each of which is associated with particular functions. In types described in Chapter 9 this phenomenon was not encountered, but in all higher plants it is a characteristic feature.

(ii) This differentiation, evident on superficial examination, is but an index of much more fundamental specialisation taking place in the more intimate details of structure. The cells of which the body of *Fucus* is composed are not all alike, but have become variously modified for the performance of different functions. This phenomenon is discussed with specific reference to *Fucus* in Chapter 21 in connexion with division of labour. The student is therefore advised to complete his study of *Fucus* by reading pages 352 to 354 after he has worked through the present chapter.

External Structure

There are several species of *Fucus*, the two most commonly encountered being the bladder wrack, *Fucus vesiculosus*, characterised by the possession of air bladders, which enable the plant to float and which explode when subjected to pressure, and *Fucus serratus*, a common brown seaweed, distinguishable by the serration of its edges. Both species normally occur together, attached to rocks in the inter-tidal region, though the *serratus* species usually forms a definite zone below *Fucus vesiculosus*. They differ further, therefore, from types previously described in being marine. A single plant, known in its entirety as the **thallus**, is divisible into three distinct regions. The base consists of a so-called **hold-fast**, taking the form of an irregular, flattened disc. By means of this the thallus becomes firmly attached to rocks, but the structure is not comparable with the root of a higher plant, since it has no absorptive function. Water, mineral salts and carbon dioxide are, in fact, absorbed over the general surface of the thallus. Connecting the hold-fast with the bulk of the thallus is a cylindrical stalk, or **stipe**, corresponding to the stem of higher plants. The remainder of the thallus constitutes the **frond**, and branches profusely. In every branch there is a distinct **mid-rib**, laterally expanded

to form a pair of **wings**. At the tip of each branch, between the distal ends of the wings, is a depression. This forked branching, characteristic of many of the lower plants, is termed **dichotomy**. It occurs as a result of the longitudinal division of a meristematic (page 244) apical cell at the tip of a branch, the two products each giving rise to a new branch. Distributed over the entire surface of the frond, except on the mid-rib,

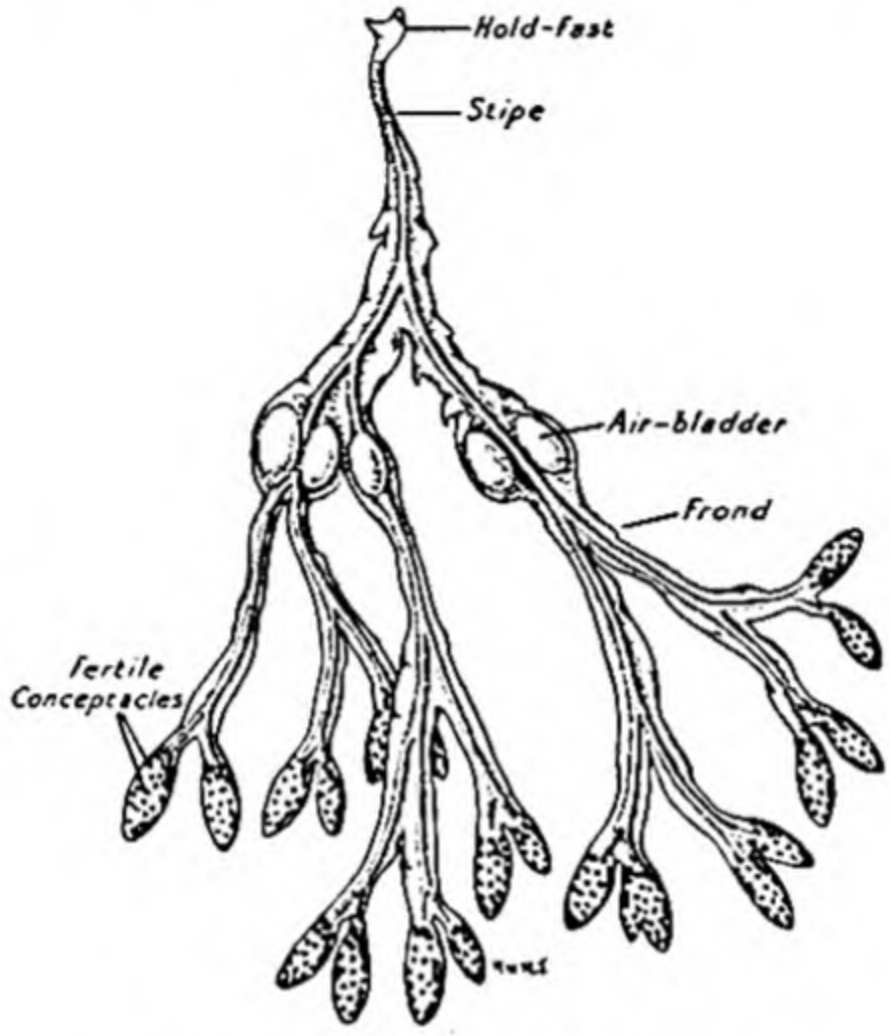


FIG. 134 – *Fucus*. An entire plant.

are numerous papillae. These mark the openings into small cavities, known as **conceptacles**. The papillae are often especially numerous at the ends of certain branches, which themselves may be considerably swollen. These are the fertile sexual organs of the thallus, whilst the smaller papillae communicate with sterile conceptacles. The function of the frond is primarily to effect photosynthesis (Chapter 23), as well as to bear the reproductive organs.

A study of the detailed anatomy of *Fucus* demonstrates the fact that each region of the thallus is considerably differentiated, in which respect it is considered further in Chapter 21. The entire surface is covered by a mucilaginous cuticle, beneath which lies the **meristoderm**, or **palisade layer**. The cells which constitute it retain their powers of division and have their axes which lie at right angles to the surface considerably elongated, whilst a peripheral layer of cytoplasm encloses a large vacuole. Embedded in the cytoplasm is the nucleus, together with a large number of **phaeoplasts**. These are comparable with the chloroplasts of higher plants, but differ from them in being olive-green or brownish in colour,

owing to the possession of an orange pigment, fucoxanthin ($C_{40}H_{54}O_6$), as well as chlorophyll. The chlorophyll itself contains less of the green pigment (chlorophyll *a* and *b*) and correspondingly more carotene and xanthophyll. The single, superficial palisade layer is principally concerned with photosynthesis. The cells of the **cortex** exhibit no particular specialisation, having larger vacuoles than those of the palisade layer,

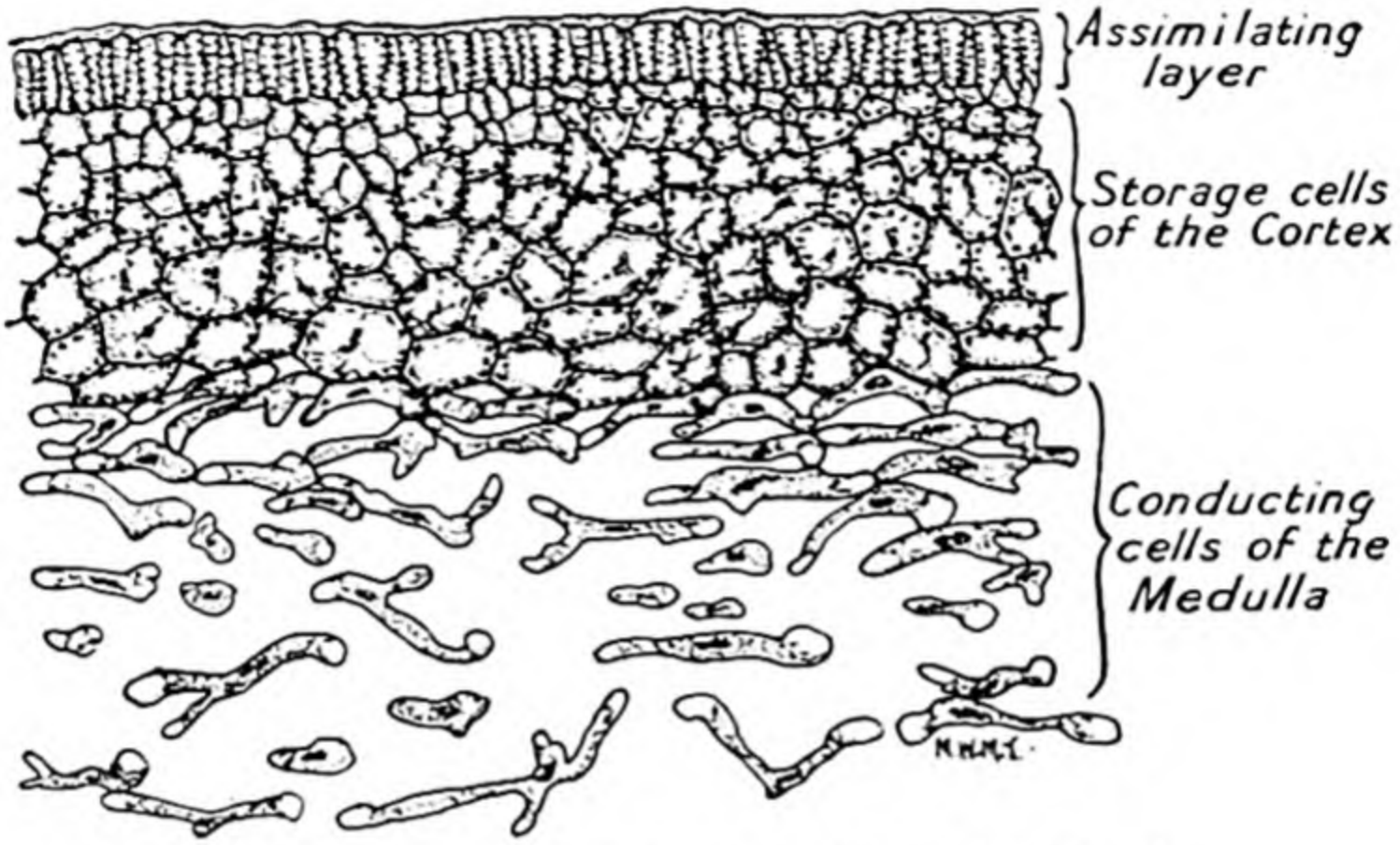


FIG. 135 – *Fucus*. Transverse section of the frond.

whilst cytoplasmic threads support the nucleus of each cell in the vacuole. In the **medulla** the cells are practically devoid of plastids. The component cells are laterally isolated from each other by mucilage, but associated longitudinally in continuous chains, as in the filamentous Algae. Groups of such cells at the outer edge of the medulla of the mid-rib are very thick-walled, and serve an important mechanical function: they are known as **fibres**, by analogy with similar cells in higher plants. These fibres are formed progressively from the innermost cortical cells, and are therefore more numerous in the older parts of the stipe. Chains of thin-walled cells are also found distributed throughout the medulla, serving for the transport of food away from the photosynthetic layer. These medullary filaments are formed just behind the apical growing point.

The cells of the stipe are similar to those of the frond. The limiting wall is several cells thick, formed by a series of divisions parallel to the surface. Thus the radial walls in this region are thick, whilst those parallel to the circumference are thin. In the medulla the number of fibres increases as the hold-fast is approached, forming the sole constituent of this latter region. In the medulla above the hold-fast occurs a number of large, vacuolated cells, lined by protoplasm, which may contain phaeoplasts. In some of the larger sea-weeds cells occur resembling

in some detail the sieve tubes of flowering plants. These medullary cells serve for the conveyance of food to the hold-fast.

All the above types of cell are formed by differentiation of the products

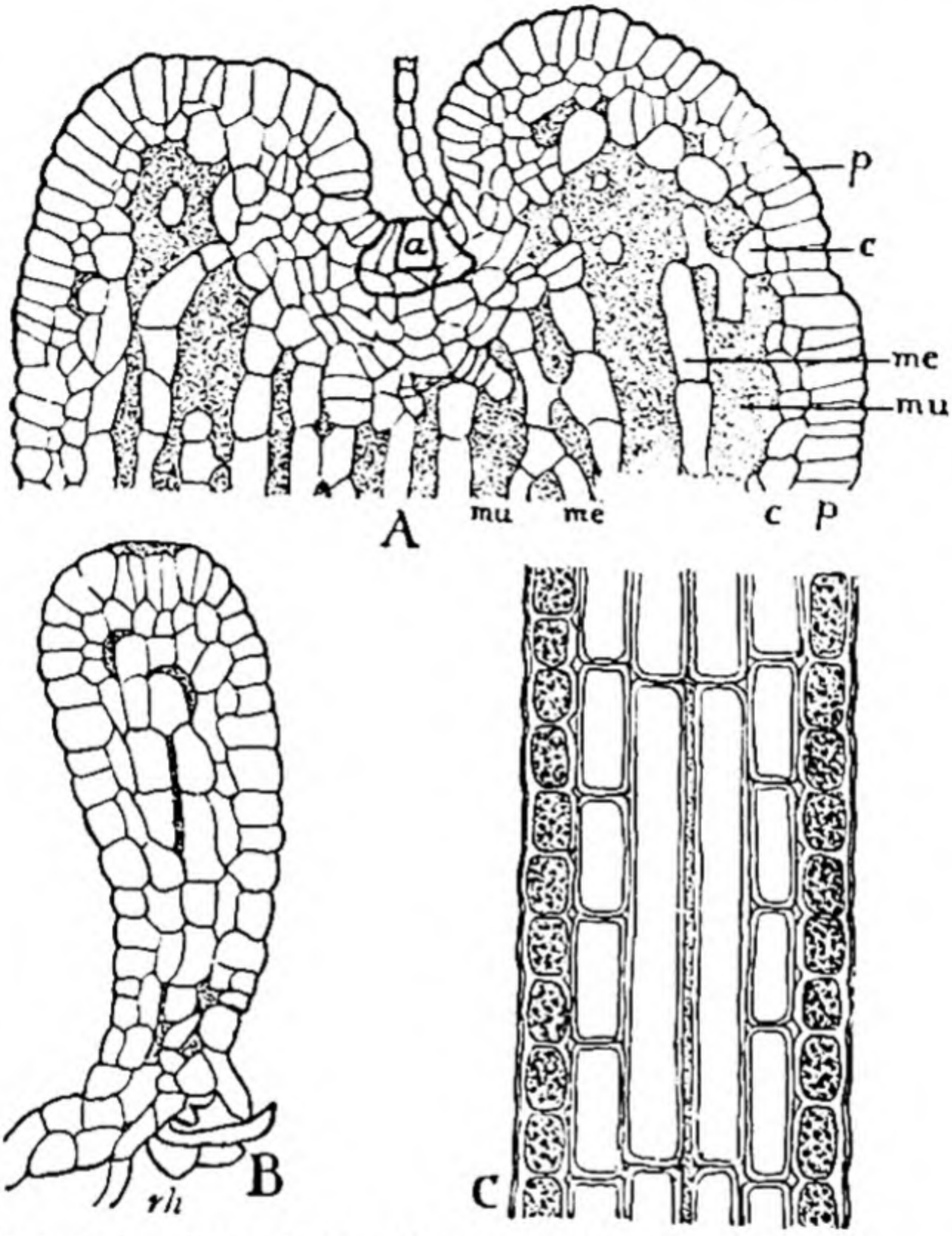


FIG. 136 – *Fucus*. (From 'Elements of Plant Biology', by A. G. Tansley and W. O. James. George Allen & Unwin.)
A., Longitudinal section through the apex of frond (the cells are in outline, the intercellular mucilage dotted). *a*., apical cell, surrounded by the cells produced from its previous divisions; *p*., photosynthetic layer; *c*., cortex; *me*., medullary cells; *mu*., mucilage from their walls. Further from the apex the cortical cells increase in size and the medullary cells in length. *B*., longitudinal section of young plant in cylindrical stage; apical groove just developing; medullary cells beginning to lengthen and to separate. *rh*., first rhizoids, which develop into 'hold-fast'. *C*., longitundinal section of part of the bristle-like thread of *Stictyosiphon*, showing dense contents and phaeoplasts of cells of photosynthetic layer, which cells are half the length of those of the cortex and a quarter of that of those of the medulla. This arrangement is due to the more numerous divisions of the surface cells. (Compare with *B*.)

of division of the unspecialised cells at the apices of the branches, as in higher plants. At each tip there is a single, six-sided cell, from which small cells are cut off by unequal division. As a result a collection of similar, thin-walled, small cells is produced just behind the apex. These cells are filled with dense protoplasm and contain many phaeoplasts. As they get pushed away from the apex by further cell-division they become differentiated according to the region of the body in which they find themselves. Thus those forming the superficial layer of the frond change in character but little, constituting the photosynthetic palisade layer. The cortical cells are produced principally by an increase in the size of the vacuoles. The innermost cells become thick-walled after their middle lamellae (page 316) have become mucilaginous, thus constituting the medulla. Such differentiation as is here witnessed may be dependent upon the position of the various tissues relative to the supply of food and oxygen – i.e. to the physical and chemical environment. The principle involved is of general application throughout the animal- and plant-kingdoms.

Life-history

Unlike forms previously described, *Fucus* never reproduces asexually. Not only so, but the gametes, and possibly the conceptacles producing them, are clearly distinguished into male and female. The same plant in some species may bear both male and female conceptacles, whilst in the two common species under consideration they occur on different plants. Simplest of all, in some species the male and female gametes are produced in the same conceptacles. The structure of the male and female conceptacles may best be understood by reference to Figs. 137 and 138. From the cells lining the male conceptacle there project into its cavity numerous much-branched hairs, whilst the aperture, known as an **ostiole**, communicating with the exterior, is also surrounded by hairs. Some of the hairs within the cavity bear the male reproductive organs, or **antheridia**. Each of these is a non-cellular body, whose contents become divided up to form some sixty-four minute spermatozoids, each of which contains one or two organge-coloured granules, known as **chromatophores**. The hairs lining the conceptacle secrete a mucilaginous fluid which, as the tide recedes, exudes from the ostiole, carrying with it the antheridia in the form of an orange-coloured mass. The spermatozoids are liberated by the rupture of the walls of the antheridia, and swim freely in the rising tide by means of a pair of lateral flagella. The base of the more anterior flagellum is partly surrounded by a funnel-shaped membrane, itself revealed by the use of the electron microscope as traversed by thirteen concentric bands. It may possibly serve ultimately for the attachment of the sperm to an egg, prior to penetration. Each flagellum is in like manner shown to be of composite nature, consisting of a number of strands, into which it may disintegrate, and beset with numerous tufts of minute hair-like structures.

A female conceptacle is normally more conspicuous from the surface than the corresponding male structure. Within its cavity is a lining of hairs, but the female reproductive organs, or **oögonia**, actually replace these hairs and are not branches of them. Certain sterile hairs which

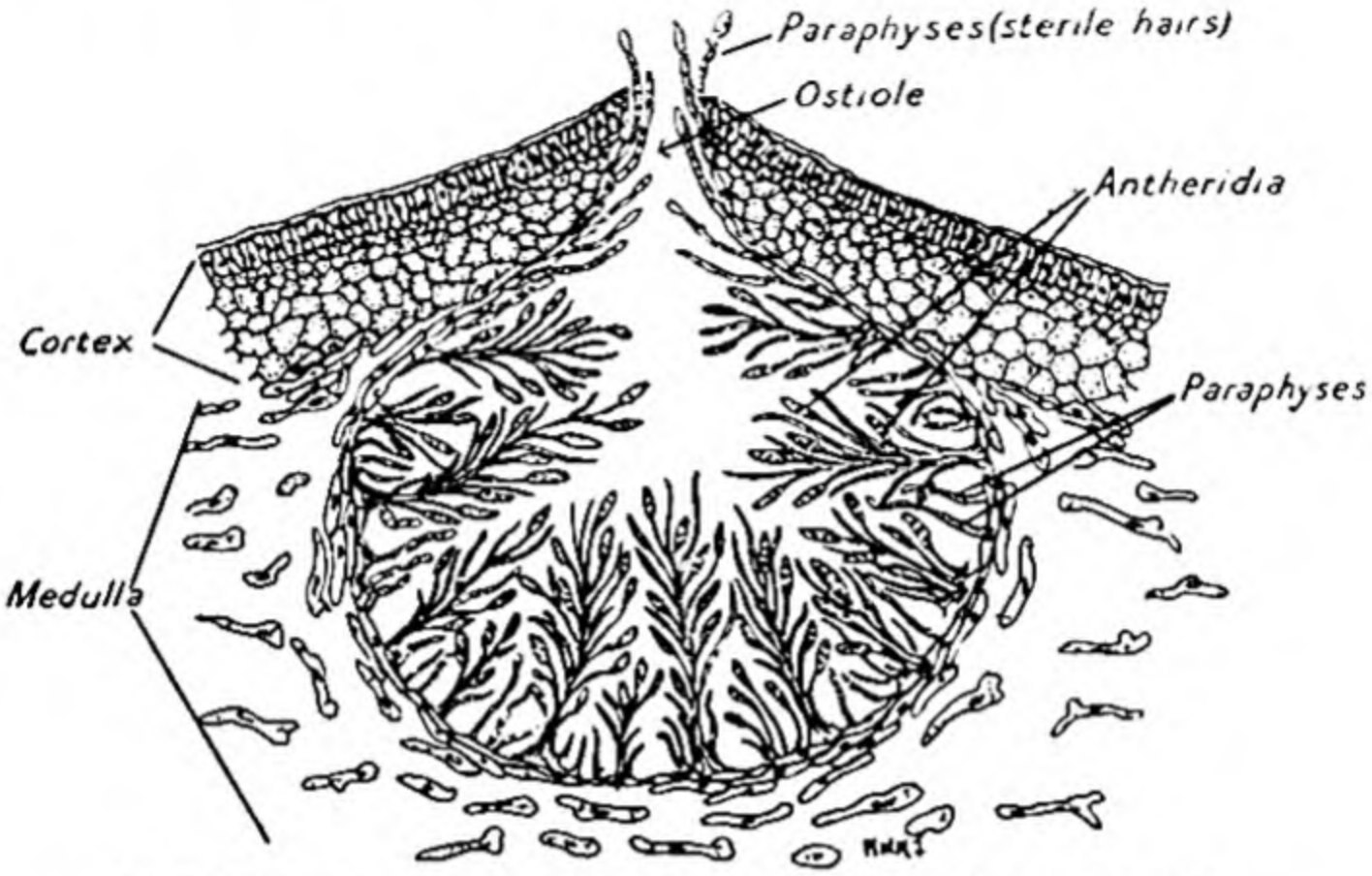


FIG. 137 – *Fucus*. Transverse section of a male conceptacle.

remain within the conceptacle are known as **paraphyses**. The nucleus of each oögonium becomes divided up into eight masses, each of which may become surrounded by a separate covering of cytoplasm. In other species the cytoplasm collects around only some of the eight nuclei, so that a correspondingly smaller number of eggs, or oöspheres, is produced. The wall of the oögonium is originally triple, but eventually the outer coat is burst by the swelling of the middle layer. This soft wall folds back, liberating the eggs still retained within the inner coat, now in the form of a bladder. Finally this also becomes ruptured, allowing the escape of the contained eggs.

The eggs and sperm, present together in the sea-water, complete fertilisation. Each egg secretes some substance which exerts powers of attraction over the spermatozoids, which swarm round it in a state of oscillation. One of them eventually penetrates the egg, after which the nuclei of the gametes fuse, so that a zygote is formed. It becomes enclosed within a wall, and in this condition constitutes an **oöspore**. It differs from the zygospores of other forms in that it is thin-walled and non-resistant, commencing to germinate almost at once. It first becomes elongated, and at one end the structure so formed becomes pointed, very soon effecting attachment to a rock by means of a secretion of mucilage. The free portion of the plant increases further in length, and soon an apical cell becomes distinguishable. By the longitudinal division of this cell dicho-

tomous branching is initiated. By continued elongation and branching a complete thallus is formed, the conceptacles arising as invaginations. The progressive differentiation of cells as they recede from their seat of formation at the apex is discussed on page 195.

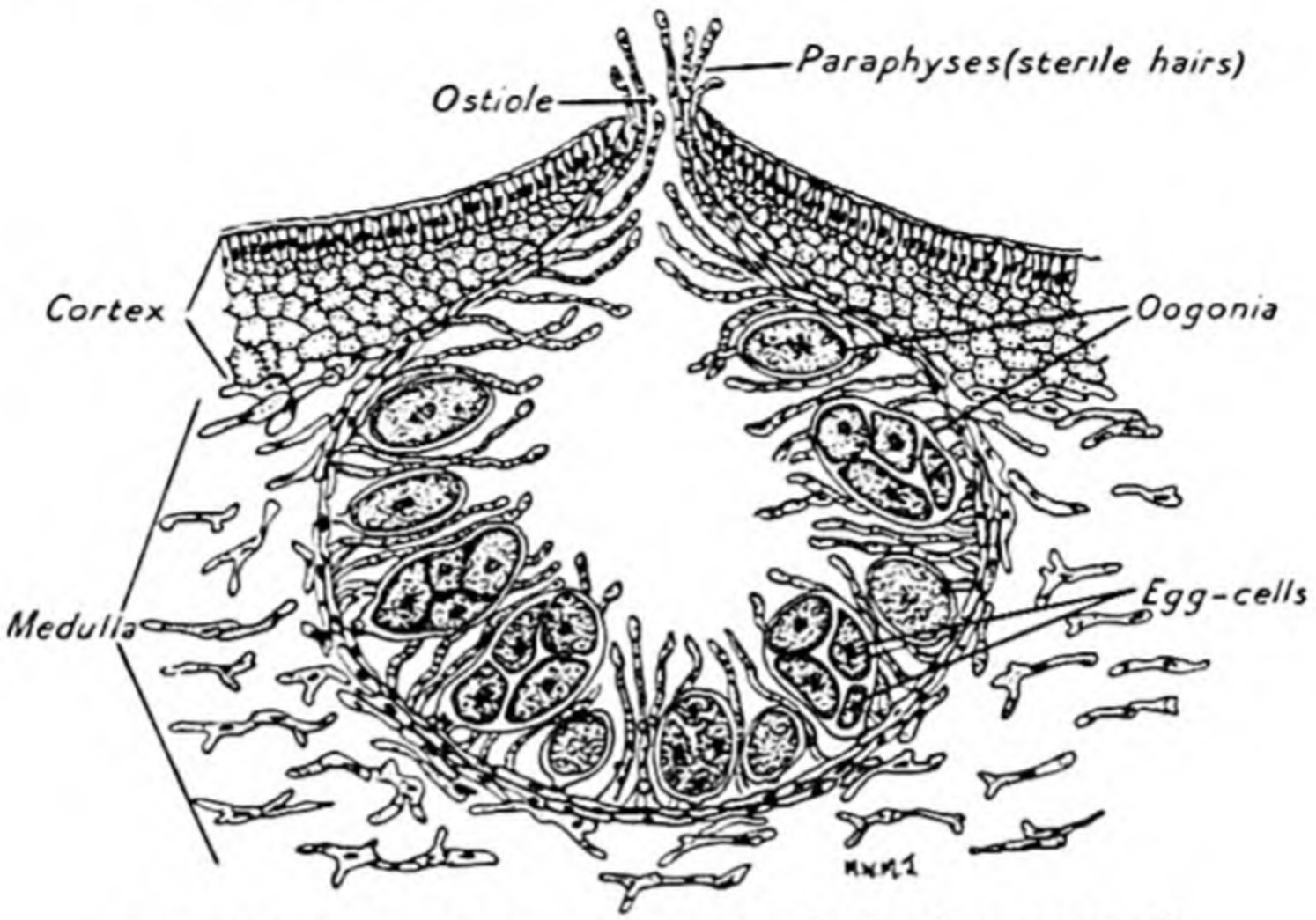


FIG. 138 – *Fucus*. Transverse section of a female conceptacle.

It is interesting to note that the cells of the thallus of *Fucus* are diploid in chromosome-content and that meiosis (page 316) occurs during gamete-formation.

PRACTICAL WORK

Examine both fresh and preserved material with a view to confirming the various external characters. A complete thallus should be obtained and the regional differentiation observed. Sketch the complete thallus.

Examine a transverse section of the frond under low power to discover the distribution of the various tissues – palisade layer, cortex and medulla – as detailed on page 193 and depicted in Fig. 135. Draw.

Examine representative portions of a transverse section of the frond under high power, noting particularly the conducting cells and the 'fibres'. Draw.

Examine similarly longitudinal sections cut one at right angles to the width of the frond, passing through the mid-rib, and one parallel to its surface. Draw.

Examine a longitudinal section through the apex of the frond, noticing particularly the meristematic, apical cell.

Examine under the low power sections through male and female con-

ceptacles. Draw. Examine the antheridia and oögonia under high power, distinguishing as many stages in development as possible. Draw.

As far as possible cut the required sections by hand with a sharp razor. Occasional reference to prepared slides is desirable to discover the required standard of thinness.

CHAPTER 11

Selected Fungi. Bacteria

As well as the Algae, examples of which were studied in Chapter 9, there is a large collection of plants, characterised by the absence of chlorophyll, also included in the Thallophyta. These colourless plants – colourless only in the sense that they do not contain chlorophyll, though they may be otherwise pigmented – are divisible into two groups, namely, the **Fungi** and **Bacteria**. The diagnostic features of each group may best be discovered by means of a study of selected examples. Owing to the almost total absence of chlorophyll they have, however, certain characteristics in common, principal amongst which is their mode of nutrition. Owing to their synthetic disabilities, they must absorb organic food in solution. This food they obtain either from dead matter, in which case their nutrition is described as **saprophytic**, or else they become dependent upon the body of some individual living organism, and are then said to be **parasites**. Exceptions are provided by the green sulphur Bacteria, which are capable of photosynthesis, utilising hydrogen sulphide instead of water, as well as by certain other Bacteria which practise a different form of synthesis – *chemosynthesis* (page 409). Examples of both saprophytes and parasites are described in the present chapter, whilst these various methods of nutrition are further discussed in Chapter 23.

I. PYTHIUM

Pythium is a parasitic Fungus responsible for the 'damping off' of seedlings grown in excess moisture. The disease is characterised by the appearance on the surface of the seedling of delicate, white threads, though by this time the disease is well advanced, for the Fungus is at first not visible externally but penetrates the tissues of the seedling. Longitudinal sections or 'squash' mounts of the seedling should therefore be cut to obtain details of the condition of the Fungus in the early stages of the disease.

Structure

The Fungus consists of a network of branching threads, each known as a **hypha**, whilst the whole system of threads constitutes the **mycelium**. Each hypha contains a mass of granular cytoplasm, vacuolated to some extent. Numerous nuclei are present, though there are no cell-walls to divide a hypha up into the usual compartments. Such a multi-nucleate

mass of protoplasm is known as a **coenocyte**. The hyphae ramify throughout the tissues of their host seedling, absorbing nourishment from them. Very soon the seedling is killed, after which the Fungus continues to live saprophytically on its decaying remains.

Life-history

Some of the hyphae eventually grow out into air, either through the stomata of the hypocotyl (page 297) or by actually piercing the cuticle. The majority of the contents of such a hypha passes into the tip, which

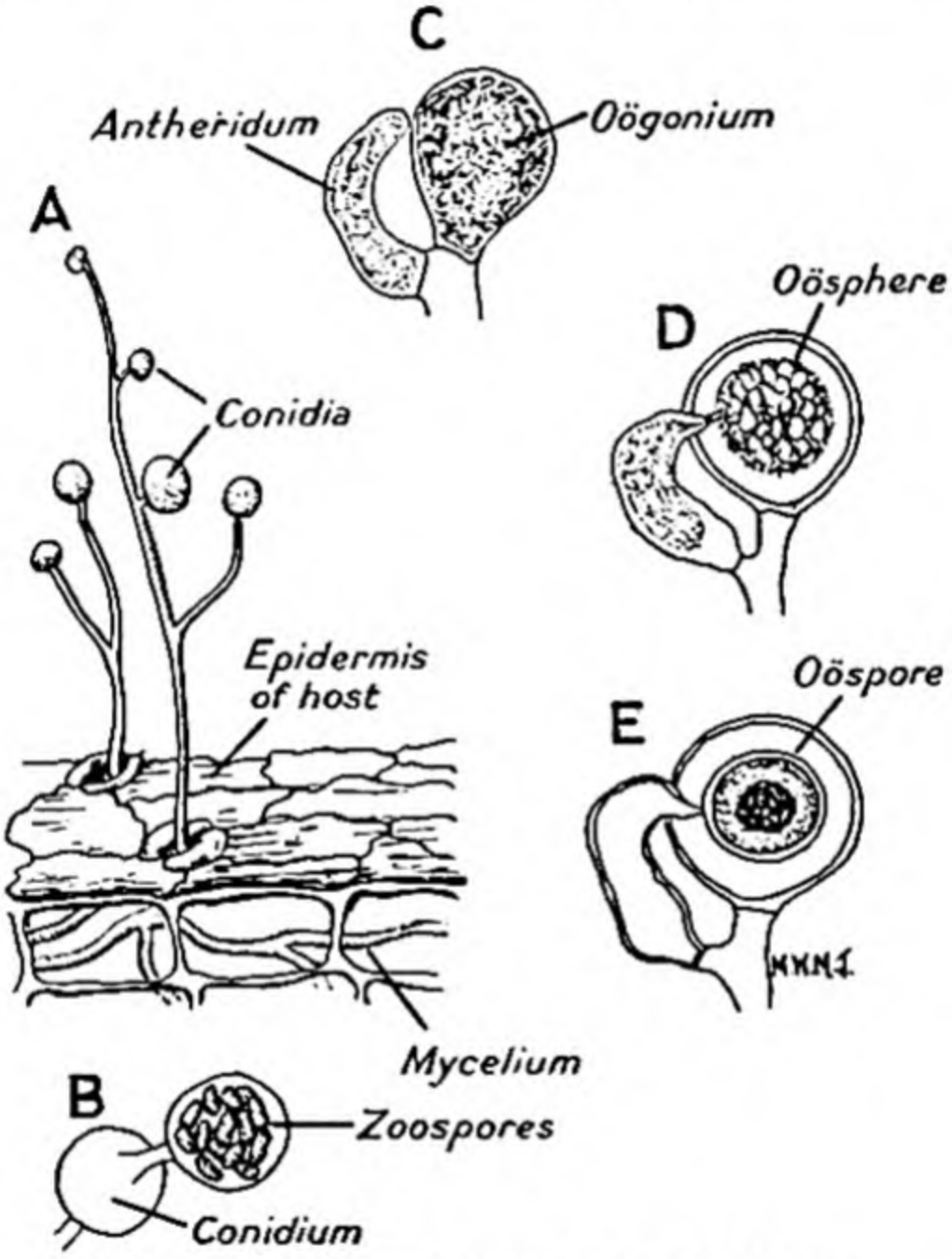


FIG. 139 – *Pythium*. Stages in the life-history.
A., section of infested cress seedling; *B*., germinating conidium; *C-E*., stages in sexual reproduction.

consequently becomes considerably swollen. It is then cut off from the remainder by the formation of a transverse wall. This body, known as a **conidium**, is liberated, and its subsequent behaviour depends on conditions. In a damp atmosphere it germinates at once, sending out a hypha to penetrate a fresh seedling and then to branch profusely with the formation of a new mycelium. If free water is actually present a swelling occurs on the conidium, and into this new swelling, known as a **zoosporangium**, pass the contents to become divided up by partitions. Each portion becomes a **zoospore**, liberated as a small, naked, biflagellate body.

Being thus provided with locomotory organs the zoospores swim about and eventually penetrate a fresh seedling, where they germinate to form new mycelia.

In these ways the disease spreads rapidly, and such asexual reproduction is continued as long as conditions remain favourable, viz., an adequate supply of moisture and abundance of food. But when conditions become adverse a new phase in the life-history appears, resulting in the formation of resistant bodies by an essentially sexual process. A swelling appears on the ends of some of the hyphae, cut off from the remainder by the formation of a transverse wall. The contents of this body, known as an **oögonium**, become granular, and a number of nuclei may be distinguished. Later a large mass of cytoplasm, containing but a single nucleus, becomes differentiated from a peripheral cytoplasm, containing the remainder of the nuclei. This central mass is the **oösphere**, or egg. The male reproductive organ usually arises on the same hypha as a lateral branch, just below the oögonium. Like the oögonium it becomes separated from the remainder of the hypha by the formation of a transverse wall, and assumes a club shape. It is known as an **antheridium**, whilst its contents become the male gamete. It grows towards the oögonium, with which it eventually makes contact. From its extremity is put out a short tube which, piercing the wall of the oögonium, eventually reaches the oösphere, with which the contents of the antheridium fuse after passage along the tube thus formed. Although the oögonium and antheridium are at first multi-nucleate, all but one nucleus in each organ degenerate, so that normal gametes are formed. The resultant zygote becomes clothed with a thick, resistant coat, and constitutes an **oöspore**. The time and manner of germination of the oöspore depends largely on external conditions. Thus the outer coat may burst and the contents at once become a new mycelium. Alternatively the contents may become divided up to form **zoogonidia**, whilst finally there may grow out from the oöspore a delicate tube, into which pass the contents before subdivision to form **zoospores**. In any case the liberated bodies attack fresh seedlings to form new mycelia.

As has already been pointed out in reference to *Monocystis*, *Plasmodium* and *Taenia*, the life-histories of parasites show certain important characteristics. Rapid propagation is effected when conditions are favourable, whilst resistant bodies are produced in cases of adversity. This is particularly evident in the life-history of *Pythium*, whilst in the cases of the animal parasites referred to above it is somewhat modified, especially in *Plasmodium*, on account of the retention of the parasite, for some period in its life-history, within an intermediate host. Nevertheless certain general tendencies are evident in the life-histories of all parasites, whether animal or plant.

2. MUCOR

Mucor is a common saprophytic Fungus, constituting one of the so-called 'moulds'. The commonest species is *M. mucedo*. It occurs on a number of organic substances, such as bread, cheese, leather and jam, provided conditions are sufficiently moist, appearing first in the form of a network of white threads, rather like a thin covering of cotton-wool.

Structure

The individual threads, known as **hyphae**, are much branched, and penetrate the substratum on which the Fungus is growing. The whole

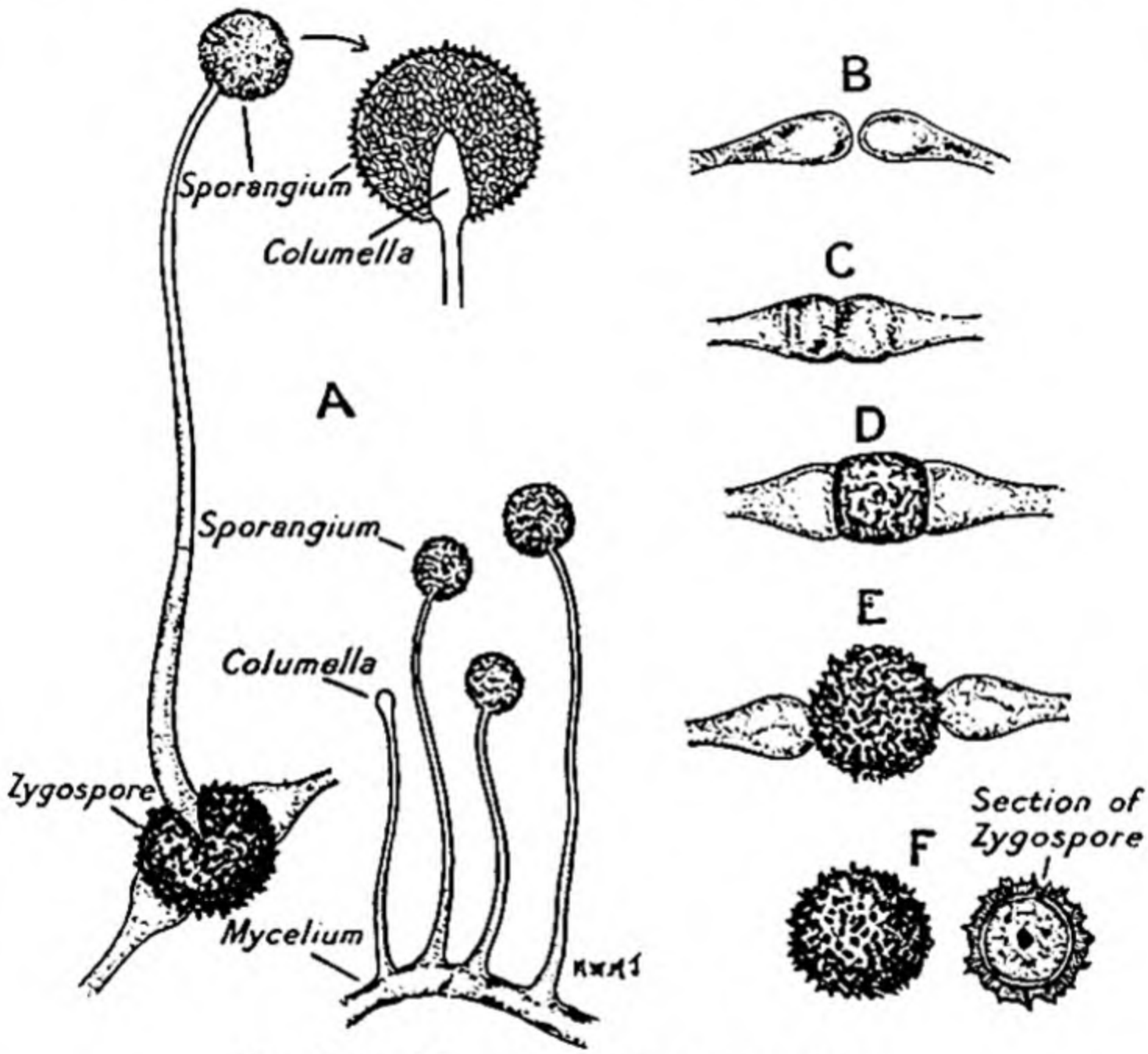


FIG. 140 – *Mucor*. Stages in the life-history.
A., asexual reproduction; *B-F.*, successive stages in the formation of a zygospore.

system of branching threads constitutes the **mycelium**. Each individual hypha is lined with cytoplasm, which encloses numerous vacuoles. These become progressively smaller towards the tip, in which region they are entirely absent. The continuous mass of cytoplasm contains several nuclei, which are not separated from each other by intervening cell-walls, so that its structure may be described as coenocytic. The lower portion

of the mycelium penetrates the substratum on which the Fungus is growing, digesting some of it with the aid of enzymes (page 389) which it secretes. In this way it provides for itself liquid food, which it subsequently absorbs. Such food consists principally of suitable sugars and nitrogen compounds (either ammonium salts or more complex substances), together with certain minerals to supply phosphorus, sulphur, magnesium, sodium, potassium and iron. Some species of *Mucor* at least must be provided with thiamin (vitamin B_1), whilst Fungi and Bacteria in general require either this or some similar growth substance. The necessity of oxygen for the healthy growth of the Fungus is evident from the fact that it occurs only on the surface of its substratum, and never in the lower layers. Mucor-yeast is able to effect fermentation in this phase, so that atmospheric oxygen is not required.

Life-history

Under favourable conditions rapid propagation occurs by asexual methods. The heads of some of the aerial hyphae become swollen, and are then separated from the remainder by the formation of transverse partitions. These partitions become arched into the swollen tips, each arched wall being termed a **columella**. The contents of the tip now become divided up into a number of small masses, and eventually the wall of the **sporangium**, as this structure is now known, bursts, setting free the **spores**, each of which is a minute,multinucleate mass of protoplasm, enclosed within a thin wall. When these spores are liberated they germinate at once on coming into contact with any substance which can provide them with suitable food. This is effected by the emergence from the spore of a delicate tube, into which pass the living contents. This branches profusely to form a new mycelium. A hypha bearing a sporangium is termed a **sporangiophore**, and is characterised by being positively phototropic (page 455). As a result it grows upwards towards the light, well away from the substratum, thus ensuring a more efficient dessemination of the spores.

A peculiar kind of resistant body, known as a **chlamydospore**, is occasionally formed by *Mucor*. A hypha becomes divided transversely into a number of lobes, the wall of each of which becomes thickened. Eventually the hypha fragments, thus liberating the chlamydospores. These germinate under favourable conditions.

At intervals in the life-history resistant zygospores are formed as a result of sexual fusion. The tips of two hyphae from the mycelia come into contact. These tips, known as **gametangia**, become swollen due to the accumulation of the contents of the hyphae there. In most species this process occurs only between hyphae of physiologically distinct, but externally identical, mycelia, described as (+) and (−). Such a phenomenon is termed **heterothallism**. The explanation of this phenomenon in genetical terms is outlined on page 583. In other species, described as

homothallic, fusion is between hyphae of the same mycelium. The tips are then cut off by transverse partitions, whilst the walls separating the two hyphae become absorbed, allowing the contents to fuse in the formation of a single mass of protoplasm. This mass becomes rounded off and clothed with a thick wall to form a **zygospore**, containing a number of nuclei and considerable food reserves. It is capable of withstanding considerable desiccation and eventually germinates to form a sporangiophore when conditions become favourable. This is effected by the rupture of the thick wall, followed by the extension of a delicate tube, into which pass the protoplasmic contents to become divided up into a number of spores, each of which may become a new mycelium on alighting upon a suitable medium. It is interesting to note that all the spores derived from a single zygospore give rise to either (+) or (−) strains, but not to a mixture.

Occasionally the process of zygospore formation fails to reach completion. In this case one of the hyphae involved may give rise to a body, termed an **azygospore**, apparently resembling a zygospore in all particulars. This process can be induced experimentally in the laboratory by, for example, high temperatures, whilst it may also follow abortive attempts at zygospore formation between hyphae of different species.

If placed in a suitable nutritive solution the hyphae of a mycelium of *Mucor* each break up into chains of cells by the formation of transverse septa. These cells either become chlamydospores (page 204) or else remain thin walled to constitute **oidia**. These latter are capable of budding and also of the fermentation of sugar solution, forming alcohol. This is known as the **Torula** condition of *Mucor* and obviously closely resembles *Saccharomyces* (page 206).

The same characteristics in the life-history of *Mucor* may be distinguished as those evident in the life-history of *Pythium*. Rapid propagation by asexual methods is followed at intervals by the formation of resistant bodies. It should be noted that, in both *Pythium* and *Mucor*, meiosis occurs in the early stages of development of the oöspore or zygospore, so that the nuclei of the vegetative phase are haploid.

3. PENICILLIUM

Penicillium, though a Fungus, belongs to a different class from that in which *Pythium* and *Mucor* are found. The **Phycomycetes**, including *Pythium* and *Mucor*, are characterised by their insignificant structural departures from the Algae, including a well-defined sexual phase in their life-history. The **Ascomycetes**, of which *Penicillium* is an example, exhibit a peculiar method of spore-formation (see later), whilst the sexual phase in the life-history is largely suppressed.

Structure

The mycelium of *Penicillium* essentially resembles that of *Mucor*, whilst both Fungi are found in similar habitats. The hyphae, however, are described as septate, since they are divided by transverse partitions into multinucleate compartments. Distributed throughout the cytoplasm is a blue-green pigment, not to be confused with chlorophyll, with which it is not in any way related.

Life-history

Under favourable circumstances aerial hyphae, passing more or less vertically from the substratum, are responsible for the formation of spores, though in a different manner from that seen in *Pythium* or *Mucor*. Instead of the tips becoming swollen to form sporangia a number of divergent branches arise, and these subsequently become further subdivided. At the ends of the finest branches chains of spores, known in this case as **conidia**, are formed. They eventually become detached and are carried away in the air, germinating when they come to rest on a medium suitable for food. Occasionally a sexual phase appears in the life-history of *Penicillium* and other Ascomycetes, whilst the occurrence of actual fusion of nuclear contents during the process has been observed. In most, however, no special sexual organs have been described. It is known that occasionally a body, termed an **ascogonium**, arises from a hypha, and this later becomes completely enclosed by branches arising from the same hypha. The contents of the ascogonium become divided up into separate cells, from each of which branches are formed, ramifying throughout the investment. One cell, known as an **ascus**, from each branch becomes divided up to form eight **ascospores**. These when liberated by the rupture of the investment of the ascogonium germinate to form new mycelia, though the ascospores may first undergo a period of rest if conditions are not favourable.

This formation of asci, and subsequently of ascospores, is one of the principal characteristics of the Ascomycetes, though, as stated above, it is not known with certainty whether or not is is preceded by a process of conjugation. Like other Fungi, *Penicillium* is propagated by spores, known in this case as conidia, as long as conditions remain favourable.

4. SACCHAROMYCES

Like *Penicillium*, *Saccharomyces* is a genius of the group Ascomycetes. Members of this genus, commonly termed 'yeasts', are of economic importance owing to their use in the manufacture of alcohol. This characteristic property is referred to on pages 435 and 439.

Structure

The mycelium consists, not of hyphae, but of a series of single cells, disposed separately or in clusters. Each cell is bounded by a thin **cell-wall**, lined with a layer of cytoplasm, which, in its turn, surrounds a large, central **vacuole**. There is no distinct nucleus, but, as a result of subjection of the cells to certain methods of fixation and staining, there

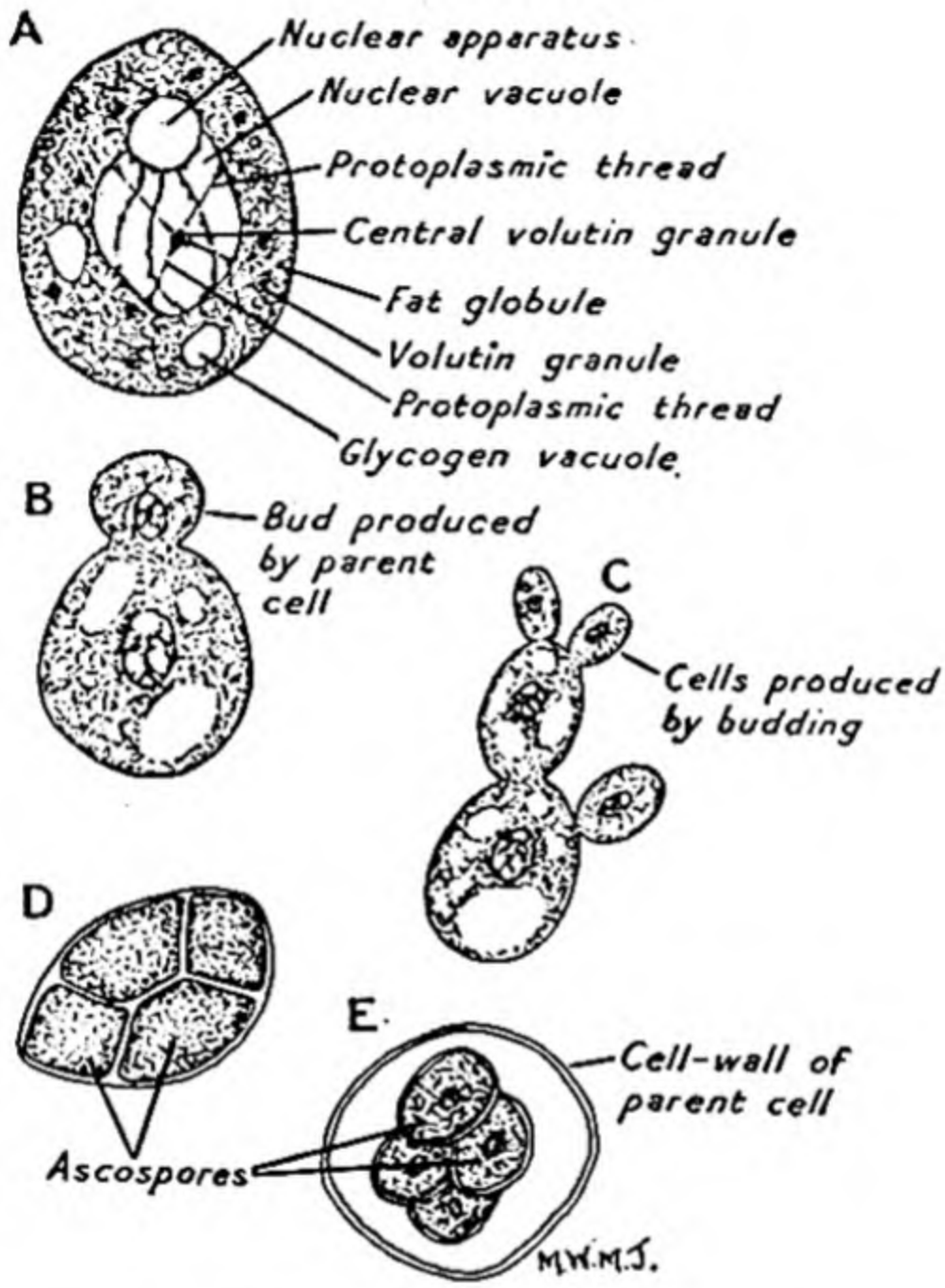


FIG. 141 – *Saccharomyces.*
A. Cell structure
B. Cell budding
C. Chains of cells produced by budding
D and E. Formation of ascospores

appear over the surface of the vacuole various sized granules and threads. These together constitute the **nuclear apparatus**. It was formerly held that the threads were of the material termed chromatin, but since the existence of this material in the living state has been shown to be unlikely, some new interpretation must be placed on these structures as they appear in yeast cells. It would appear probable that *Saccharomyces* is degenerate in nuclear structure, and that, whilst containing the normal chromosomal material, this is not confined within a nuclear membrane,

as it is in the vast majority of animal and plant cells. The threads described may well be as much artefacts of cytological method as were the structures whose apparent existence occasioned the suggestion that normal nuclei contained chromatin granules. As well as the nuclear apparatus, the yeast cells contain certain reserves of food. Thus there may frequently be observed large **glycogen vacuoles**, and in addition certain small bodies, termed **volutin granules,** which stain deeply with methylene blue.

Life-history

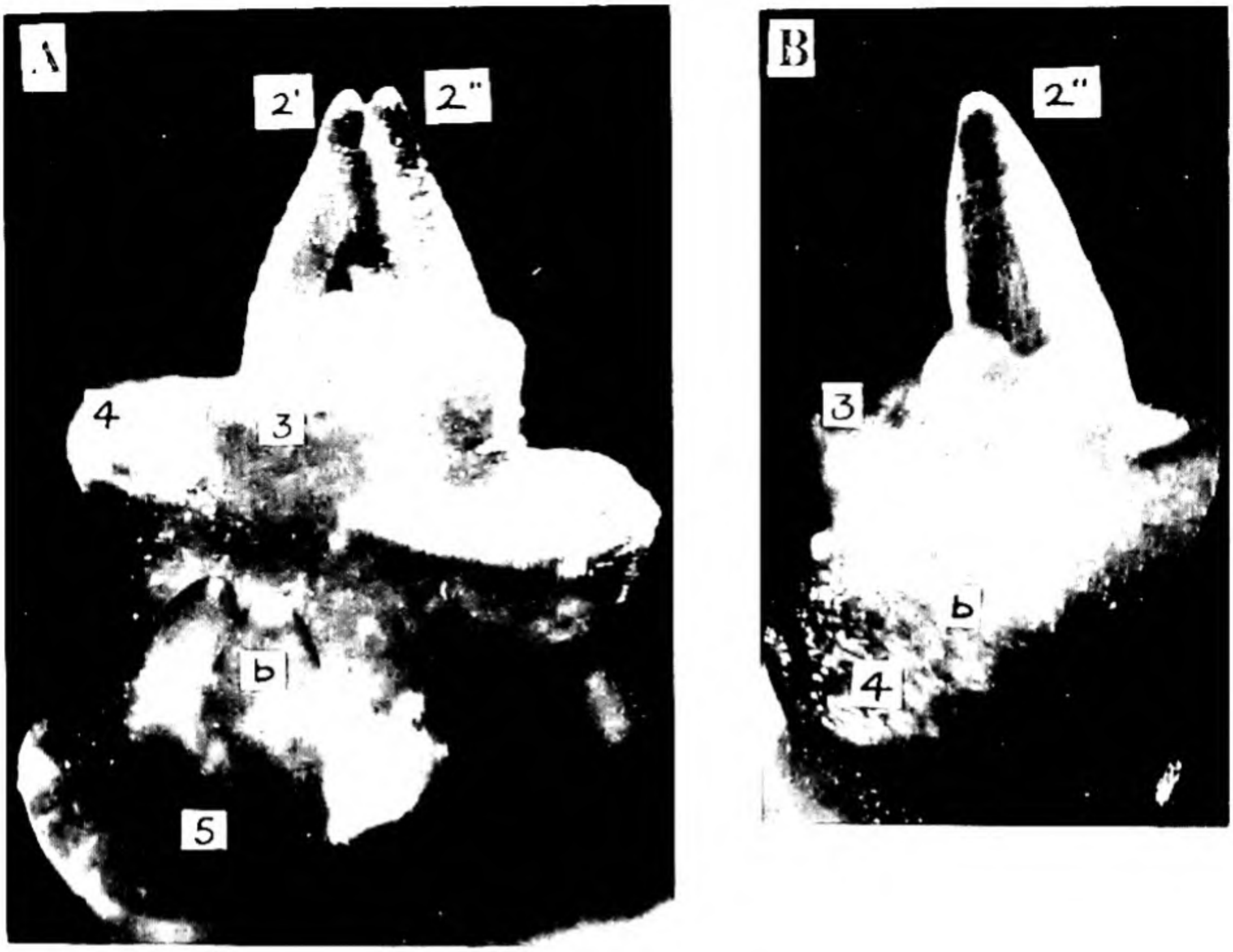
Most commonly in the family *Saccharomyces*, reproduction is purely asexual, taking place by a process of budding, or **gemmation**. A small outgrowth arises from a single cell, and this bud gradually assumes the form and size of the parent cell, from which it becomes separated by constriction. Rapid reproduction by this means results in the formation of clusters of cells, secondary buds arising before separation of the primary ones is complete.

Sexual reproduction has been observed in the genus *Schizosaccharomyces*, and in certain other genera. In the genus mentioned, two cells conjugate to form an **ascus**, from the diploid (page 313) nucleus of which eight haploid **ascospores** arise. Following their liberation, each ascospore germinates to form a new vegetative cell. In certain other genera, four, instead of the normal eight, ascospores are formed, and these frequently arise by parthenogenesis (page 583) without previous conjugation. Finally, in some genera of yeasts the process of spore formation has been completely suppressed.

Conclusion

In general, it is apparent that the members of the family Saccharomyces show various degrees of degeneracy. They are, like all other Fungi, characterised by the absence of chlorophyll, which results in their nutrition being essentially of the saprophytic type (page 408). Only very few species – e.g. *Saccharomyces Ludwigii* – are still capable of forming true hyphae, and then only in special nutritive conditions. Reference has already been made to their degeneracy in nuclear structure. In their life-history the sexual phase shows progressive reduction to its final disappearance in the asporogenous forms.

Yeasts are of commercial importance on account of their ability to effect the fermentation of sugars, as described on page 435. The chief products are ethyl alcohol and carbon dioxide. The source of the sugar varies with different alcoholic beverages. Thus beer is produced from malt (*i.e.* germinated barley), whilst total fermentation of the sugar obtained from the starch in malt, followed by distillation, results in the production of whisky. Brandy is manufactured by the fermentation and subsequent distillation of grape-juice.



Early stages in leaf development. Photomicrographs of apex of privet. (*A*) The third, fourth and fifth leaves have been removed. The second pair of leaves (2′ and 2″) is visible and, between them, one leaf of the first pair. At *b* are the first two leaves of a lateral bud. (*B*) One of the second leaves (2″) and the first pair of leaves. (*C*) Leaf 2″ has been removed and the apex is viewed from the side. The shoulder 3 marks the position of the insertion of the third leaf, and *b* is one of the two first pairs of leaves in the axil of the fifth leaf, corresponding to that seen in (*A*). (*D*) is a view of (*C*) from above, showing the apex as a shining, more or less rectangular, platform between the first pairs of primordia: 2, 3 and 4 mark the position where the primordia of pairs 2, 3 and 4 were inserted. The scale line below (*B*) represents 0.5 mm. (By courtesy of Sir Eric Ashby and Dr B. C. Sharman. From *Endeavour*, No. 29. I.C.I. First published in *The Naturalist*.)

Left Resting nucleus of a salivary gland cell in the fly *Drosophila melanogaster*. The genes have undergone eight cycles of reproduction and so occur as series of flat plates each with 256 genes. The larger genes make deeper staining bands. (X 1,500.) (By courtesy of Prof. C. D. Darlington. From *Endeavour*, No. 3, I.C.I.) *Right* Electron micrograph of the virus of tobacco necrosis (X 20,000). (By courtesy of Dr Kenneth M. Smith. From *Endeavour*, No. 13, I.C.I.)

Electromicrograph of *Streptococcus viridans* (X 30,000). This green-producing group embraces such forms as fecle streptococcus, or *enterococcus* group, those which normally inhabit the mouth and throat and are non-pathogenic. (Quoted from *The Doctor's Book of Micro-biology*, 17th Edition.) (By courtesy of Messrs Upjohn Ltd.)

5. AGARICUS — PSALLIOTA

Agaricus, a genus containing mushrooms and toadstools, belongs to the class of Fungi known as the **Basidiomycetes**, members of which are characterised by the complete absence of sexual organs, as well as by a peculiar mode of spore-formation, in which a a number of spores, usually four, is developed from each spore-mother cell. The majority of them are saprophytes, though parasitic forms occur.

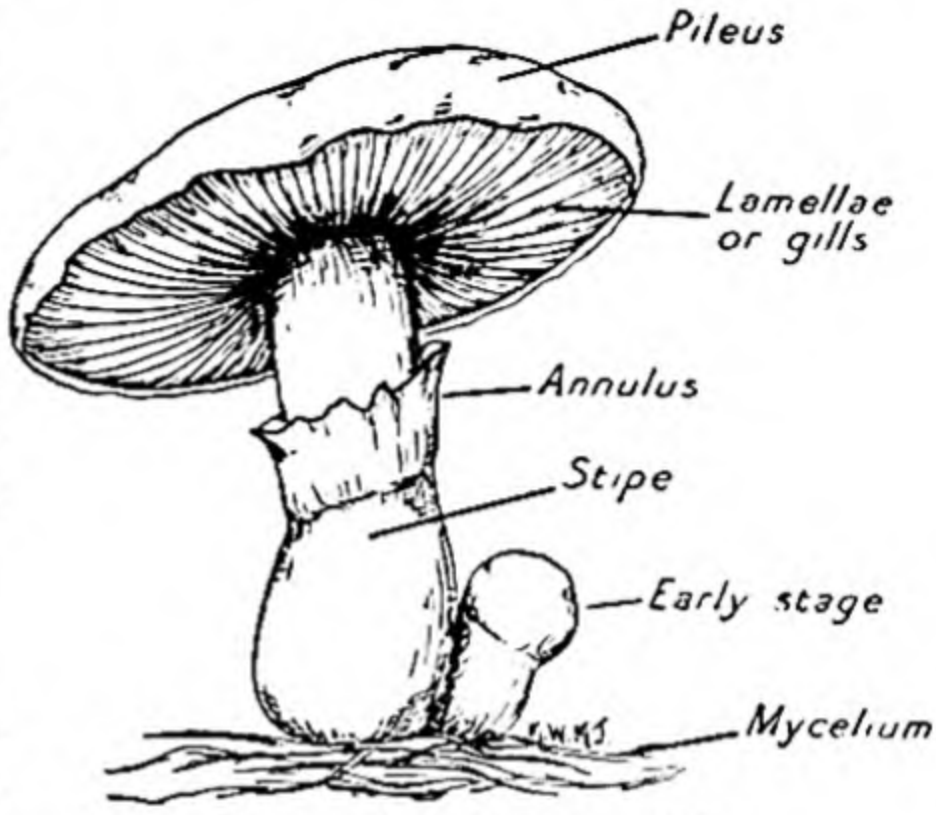


FIG. 142 – *Agaricus*. Entire.

Structure

The common mushroom lives on decaying humus, and is found in open grassland. A single sporophore of the Fungus as normally purchased, consists of a stalk, or **stipe**, on the end of which is borne a cap, or **pileus**. Surrounding the stipe is a jagged frill, or **annulus**, previously connected with the free edge of the pileus, prior to the latter's becoming expanded. The under-surface of the pileus consists of a number of radial plates, concerned in the formation and liberation of spores. The plates, known as **gills**, vary in length, some extending completely across the pileus and others for only a short distance. The stipe itself consists of interwoven hyphae, containing granular protoplasm and divided by partitions into compartments. Each hypha is multinucleate, whilst its whitish colour is due to the presence of crystals of calcium oxalate. The stipe is continued into the ground in the form

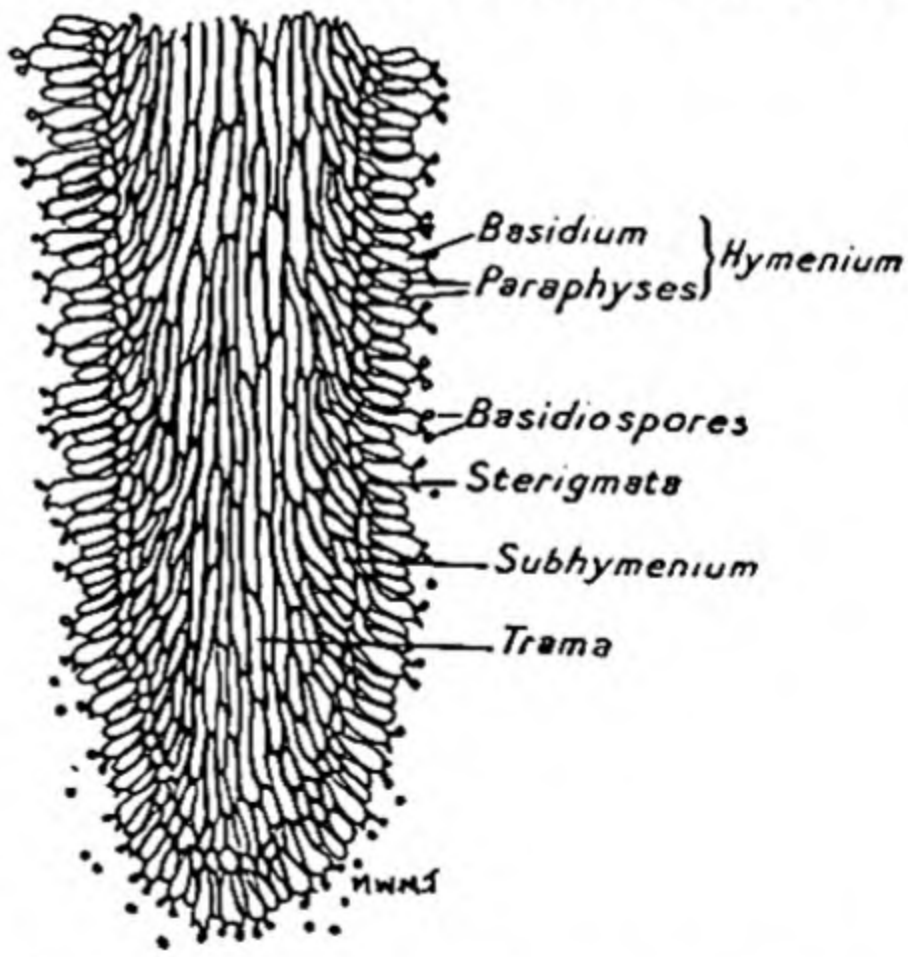


FIG. 143 – *Agaricus*. Longitudinal section of a gill.

of a branched, septate mycelium, penetrating for some distance into the soil and absorbing the humus products.

Life-History

The central tissue of each gill, constituting the **trama**, is formed by interwoven hyphae. The hyphae curve outwards on both sides, and are covered by a layer of smaller cells, constituting the **subhymenium**. The surface of each gill is known as the **hymenial layer**. It consists of cells of two kinds. Some are narrow and of uniform diameter throughout: they are known as **paraphyses**. Others, much larger and longer, are known as **basidia**. They bifurcate at their free ends to form two short, hooked processes, known as **sterigmata**, each of which becomes swollen terminally to form a single **basidiospore**. These spores develop thick coats and are soon liberated to form fresh mycelia. Thus the cultivated *Agaricus* differs from most Basidiomycetes in the formation of only two basidiospores from each basidium, instead of the usual four. In the typical condition, where basidiospores are produced in groups of four, a very interesting sequence of nuclear events takes place during their formation. The cells of the mycelium of *Agaricus* contain as many as twelve nuclei, and this number decreases progressively in the reproductive region until finally, in each young basidium, only two nuclei are found. These subsequently fuse and, after a short resting stage, this diploid nucleus undergoes two typical meiotic divisions, each of the four haploid products passing along its sterigma to become the nucleus of a basidiospore. Thus the nuclei of the plant itself must be haploid. This fusion of nuclei in pairs prior to the formation of basidiospores must represent a vestigial sexual phase in the life-history. In practice, of course, mushrooms are propagated for commercial purposes vegetatively from portions of the mycelium.

BACTERIA

Last of the subdivisions of the Thallophyta to be considered are the **Bacteria**. Their evolutionary relationships with others forms are obscure, but they are probably degenerate rather than primitive. They are of primary importance in the economy of nature, for they are responsible for most of the significant changes which take place in respect of the organic content of the soil, as discussed on page 410. Others are important to man. Thus large groups of Bacteria are pathogenic, being responsible for various diseases, whilst some are employed by man to effect certain fermentation processes, such as the 'curing' of tobacco and the 'ripening' of cheese.

Structure

A single cell consists of a minute mass of protoplasm. No separate nucleus can be distinguished, but the whole of the protoplasm absorbs

nuclear stains. It is probable that the nuclear material is distributed throughout the cell and not confined to a specific region, as in the cells of most other plants and of animals. Fat and glycogen have been identified in the protoplasm of the cells. The boundary wall of bacterial cells is

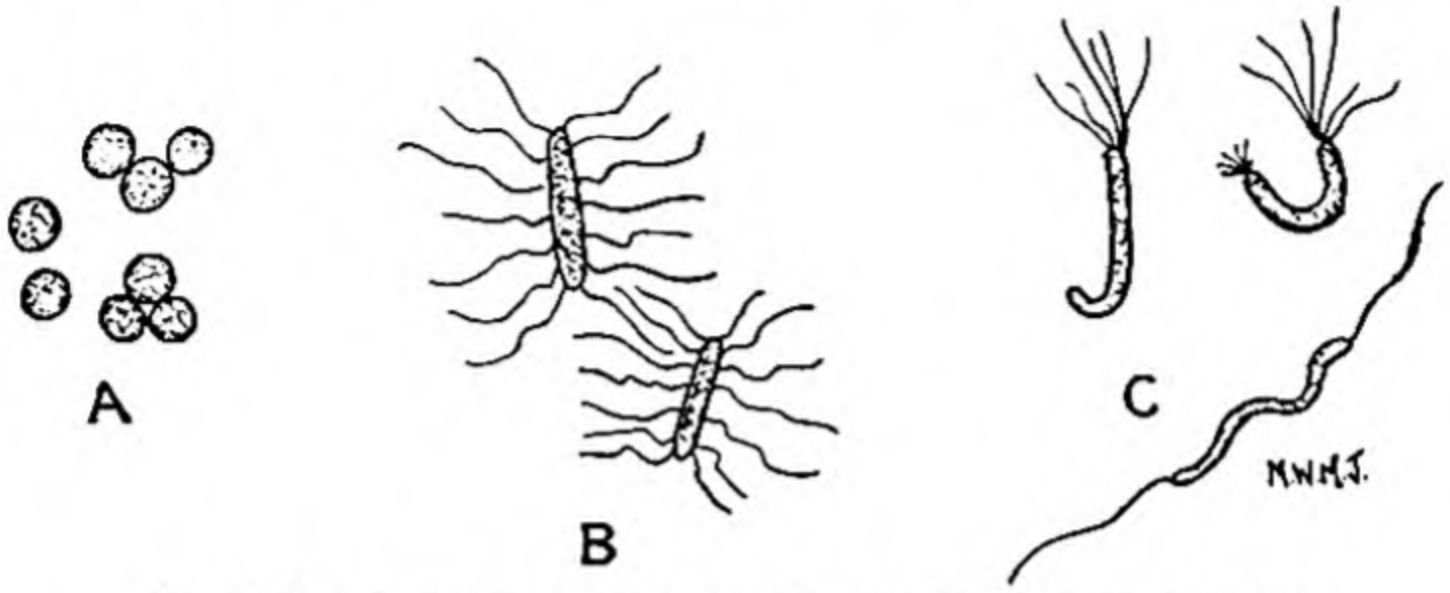


FIG. 144 – *Bacteria. A.*, Coccus; *B.*, Bacillus; *C.*, Spirillum.

somewhat variable in composition. There is always present a plasma membrane (page 304), covered with a thicker wall, of importance on account of its permeability to nutrients and metabolites. It consists mainly of lipid material, associated with protein, carbohydrates and mucopeptides. The last-named are highly insoluble and impart rigidity to the cell. Another wall component, recently investigated, is the teicholic acids. These consist of glycerol or ribitol residues, joined by phosphate groups and with sugars attached; *d*-alanine residues are linked with some of the hydroxyl groups. It is tentatively suggested that these teicholic acids may regulate the transport of metabolites and ions, or possibly be concerned with the synthesis of mucopeptides. It is believed that penicillins adversely affect the biosynthesis of this wall, which is itself regarded as the principal source of antigens (page 357). For further reading on the topic the student is referred to the article entitled *Teicholic Acids and the Bacterial Cell Wall*, by Dr J. Baddiley, published in *Endeavour*, No. 88, Jan., 1964, by I.C.I.

In many cases the entire cell is enclosed in a mucilaginous capsule, as a result of which a large number may fuse together into a mass, or **zoogloea**, visible to the naked eye.

Bacteria are roughly classified into a number of groups according to their shapes. The *bacillus* assumes the form of a straight, cylindrical rod. The *spirillum* is a curved rod, the curvature often extending to the formation of a spiral. The *coccus* is spherical in shape, with a diameter of about .5μ. Separate cells often become associated together in pairs (*diplococci*), chains (*streptococci*) or bunches (*staphylococci*). Some idea of the minute size of Bacteria may be gained from the fact that it would take about 25,000 *cocci*, placed side by side, to form a diameter to a half-penny.

Life-processes

The nutrition of the Bacteria is either saprophytic or parasitic, though reference is made on page 409 to a peculiar process, termed chemo-synthesis, enabling forms which exhibit it to derive their energy by the oxidation of inorganic substances. The energy requisite for the effecting of growth and locomotion is variously obtained. Some forms are aerobic, utilising atmospheric oxygen in the normal process of respiration. To others the presence of oxygen is fatal, and these obtain energy by various fermentation processes. Such anaerobic respiration is discussed in Chapter 24.

Life-history

When a suitable medium becomes infected with bacterial spores germination of the latter occurs. The development of the culture passes successively through four phases, as follows:

(i) *Lag phase.* The organisms accustom themselves physiologically to the medium, and multiplication is slow.

(ii) *Logarithmic phase.* The rate of multiplication rises logarithmically to a maximum. In this condition successive fissions may be completed in 30 minutes. It is small wonder, therefore, that symptoms of a disease caused by Bacteria develop so rapidly.

(iii) *Stationary phase.* Here the organisms are becoming adversely affected by metabolic end-products, and the rates of death and multiplication are approximately equal, so that no change in total numbers occurs.

(iv) *Phase of degradation.* The metabolic end-products have now accumulated in sufficient quantities to bring about a decline in numbers, with the ultimate death of all the vegetative forms.

Survival is ultimately effected by the formation of **spores**. These are spherical or oval bodies, formed within the vegetative cells and their shape and position are constant for a given species. They are extremely resistant, being able to withstand desiccation for 15 years or subjection to dry heat at 150° C. for two hours without destruction. They are, however, more susceptible to treatment with chemical substances, known collectively as antiseptics. These are of the utmost importance in surgery, and the discovery of the activities of Bacteria, and their control, has made possible a great reduction in the death-rate due to blood-poisoning following surgical operation.

Bacteria and Disease

The noxious effects produced by Bacteria upon their hosts are due to the liberation of poisonous substances, known as **toxins**, into the blood-vessels, for example, of higher animals. The toxins are of protein nature and are intensely poisonous. An animal resists an attack of pathogenic Bacteria in several ways. This problem is discussed fully on page 357.

Pathogenic Bacteria are highly specific, both in the toxins they produce and in the parts of the body which they infest. Thus the diphtheria *Bacillus* can live only in the throat. Similarly a given bacterium can often live only in a very few species of mammals, for example, so that certain diseases become characteristic of certain mammals.

Preservation of Food

Amongst other important practical application of the knowledge of the activities of Bacteria are the various devices employed in the preservation of food. They all aim at making impossible the existence of Bacteria. Thus meat and fruits may be canned. This consists in subjecting them to a given temperature for a certain period of time, thereby destroying any bacterial spores present, the product being contained in an air-tight can. The heat-process is less for fruit than for meat because of the former's acid nature. If the process of preservation is incomplete any surviving spores will germinate. The gaseous products liberated by the Bacteria will often cause the tin to bulge at the ends. Such incompletely preserved food may be dangerous to eat. Botulism is a form of poisoning which may so result. It is caused by *Clostridium botulinum*, and its effects are often fatal.

Fruit may be made into jam. In this case the sugar acts as a preservative: the osmotic pressure (page 377) of the solution is presumably too high for the Bacteria to become active. The same principle is involved in the drying of fruits. Similarly, salt is frequently used as a preservative for meat.

Since cattle are often subject to tuberculosis it is important that milk should be sterilised. This is done by a process known as pasteurisation, the milk being maintained at a temperature of 68° C. for some 30 minutes and then rapidly cooled. This treatment is sufficient to destroy any vegetative form of the tubercular *bacillus* which may be present.

Cultures

For investigation of its structure and reactions it is often necessary to obtain a pure culture of a particular Bacterium, free from others. This is done by the addition of Bacteria – perhaps many species together – to a quantity of gelatin or agar-agar. Suitable food for the Bacteria is added. The whole medium is warmed to liquefying-point, so that the individual cells may become widely separated. The medium is then allowed to set. Though thus deprived of their powers of locomotion the Bacteria divide, and soon small groups are visible, possibly to the unaided eye. Several such groups may be treated similarly with a fresh lot of the medium, and by repetition of this process pure cultures may at length be obtained. It is, of course, essential that all materials employed should first be thoroughly sterilised.

Viruses

It is appropriate at this point to make mention of viruses, commonly recognised nowadays as responsible for many diseases of both animals (e.g. the common cold, influenza, distemper in dogs, and foot and mouth disease in cattle) and plants (*e.g.* leaf mosaic in raspberries and cucumbers, and leaf-roll in potatoes). Virus particles are exceedingly minute – possibly no more than two-millionths of a millimetre in diameter. They are of nucleoprotein nature and may be regarded as homeless genes (or groups of genes), capable of self-duplication only when resident in the tissues of a living organism, within which, once established, they create havoc with the enzymic pattern of behaviour. Many viruses have been isolated and obtained in crystalline form.

The so-called **Bacteriophages** are regarded as a special type of virus. Each particle consists of a head, which is a container of *DNA*, and a tail, the function of which is attachment of the particle to a cell about to become infected and the subsequent injection of *DNA*. As with other viruses, bacteriophage particles immediately take over metabolic control, synthesising their own diagnostic protein. They multiply rapidly and the products are set free to infect further cells.

PRACTICAL WORK

Pythium

Sow cress seeds closely packed on blotting paper kept continuously wet and covered. Mount a seedling on a slide and examine the hypocotyl. Press a cover-slip hard upon the seedling, thus forcing some of the aerial hyphae away from the hypocotyl. Look for conidia. Examine older, decaying seedlings, when sexual organs may possibly be seen. Cut longitudinal sections of the hypocotyl and examine hyphae under high power. Make representative drawings.

Mucor

Soak a piece of bread in water and leave it for some days under a covered bell-jar. As a result mycelia of *Mucor* become apparent, recognisable from various other moulds present by the white colour of the hyphae. Tease out a small portion of the bread on a microscope slide and examine the hyphae of *Mucor* under low and high power. Note the presence of sporangia, borne on sporangiophores. Draw some hyphae and developing sporangia. Some of the older specimens may contain burst sporangia, in which the columella should be discovered. If possible obtain representative stages in the development of the sexual organs. If they cannot be found draw them from a prepared slide.

Obtain + and − strains of heterothallic *Mucor* (as may be purchased). Prepare a dish of raisin agar and cover while cooling, so as to keep it moderately sterile. Infect with the strains of *Mucor* at points about one inch apart. After two or three days the mycelia meet, and later a distinct black band between them indicates where the zygospores have been formed.

Penicillium

Penicillium, identifiable by its blue-green colour, is obtained in the same way as *Mucor*, and should be similarly examined. Pay special attention to the conidiophores and conidia.

Agaricus

Examine and draw *Agaricus* in successive stages of development. Examine prepared slides of sections through the gills, looking for the details of structure given on page 209. Draw.

Bacteria

Practical work on Bacteria is difficult owing to the small size of the material. Vast numbers of Bacteria of several types may be obtained by allowing a dead frog or other animal to decay in a jar of water. Prepared slides, and possibly cultures, of others may possibly be available from a pathological laboratory. Examine transverse sections through the root-nodules (page 411) of a leguminous plant, when the bodies of *Rhizobium* may be seen under oil-immersion. Place some slices of potato in water and leave to soak. Examine later a drop of the liquid near the potato, using oil-immersion. *B. mesentericus* may possibly be seen in motion. Make an infusion of hay in warm water and examine later. *B. subtilis* may well appear in the infusion.

Boil a dilute solution of sugar in a round-bottomed flask for about fifteen minutes. When boiling put a plug of cotton-wool in the neck. Leave to stand for some weeks. No apparent change occurs. Deal similarly with a second flask of sugar solution, except that no plug of cotton-wool is to be placed in the neck. After a short time it will be evident that fermentation is taking place, due to the entry of bacterial and fungoid spores. A third flask with similar contents has a plug of cotton-wool placed in the neck, but the solution is not previously boiled. Fermentation will probably occur, since spores may have existed in the air, in the flask or in the solution itself.

A series of instructive experiments is to be found in Vol. XXVI, No. 98, page 58, of the *School Science Review*, by Dr A. H. Campbell.

CHAPTER 12

Pellia. Funaria. Dryopteris

Attention must now be turned to two groups of plants at a higher stage of evolutionary development than the Thallophyta. The first of these is the **Bryophyta**, including two classes, namely, the **Hepaticae** (Liverworts) and **Musci** (Mosses). In their development there are two clearly-demarcated stages, each of which eventually gives rise to reproductive bodies. One of these generations gives rise to spores, and is consequently described as the **sporophyte**, whilst the other produces sex-cells, or gametes, and is therefore styled the **gametophyte**. The regular alternation of these two generations in this and subsequent groups of the plant-kingdom is an extremely important evolutionary phenomenon, and is discussed more fully on page 557. An example of a liverwort and a moss will now be described.

PELLIA

Pellia is a common liverwort found normally near streams, or even in shallow water, though it can survive in moderately dry conditions.

Structure

As in lower forms the plant consists of a flat, green **thallus**, attached to the ground by numerous hair-like rhizoids, emanating from a central mid-rib and functioning for absorption as well as anchorage. The thallus itself is much branched and of wavy outline. The thallus consists actually of parenchymatous cells (page 321). The epidermis has a thin cuticle, at least on the under-surface of the thallus, whilst the hairs referred to above emerge also from the lower layer as hollow outgrowths of single cells, something like a true root-hair in appearance. The cells of the mid-rib are slightly elongated and their walls somewhat thickened. Branching takes place much as in *Fucus*, being dichotomous and facilitated by division of a single, apical cell at the tip of each branch, immediately surrounded by a number of cells which secret mucilage, thus preventing desiccation.

Reproductive Organs

In early summer a number of dots may be seen distributed over the surface of the thallus. These indicate the position of the reproductive organs. The **antheridia** (male) are situated near the mid-rib about the

middle of the length of the thallus, whilst the **archegonia** (female) occur nearer the growing tip. The two sets of organs appear successively, not simultaneously. Each antheridium arises from a single, superficial cell, which first becomes divided transversely, the lower product giving rise to a short stalk by further division and the upper to a sperm mother-cell.

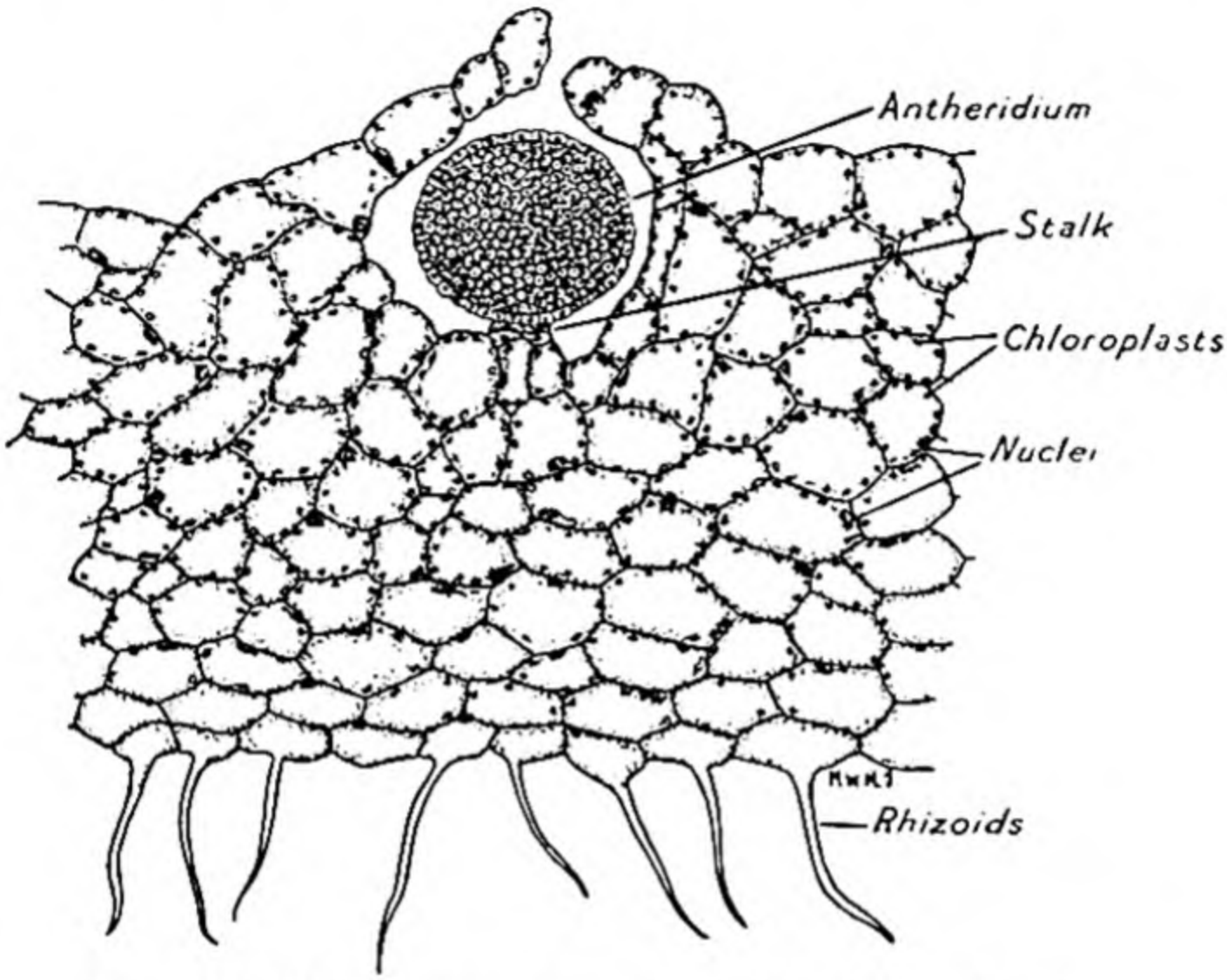


FIG. 145 – *Pellia*. Transverse section of the thallus, showing an antheridium.

The whole becomes enclosed within a flask-shaped concavity by the multiplication of surrounding cells of the thallus. Within the antheridium, spermatozoid mother-cells give rise each to a single **spermatozoid**, a spirally-coiled structure, consisting mainly of a single nucleus and bearing terminally a pair of flagella. An archegonium develops similarly, though subsequently. The structure itself is flask-shaped and not ovoid, as is the antheridium. It consists of a narrow **neck**, the wall of which is composed of some five or six single rows of elongated cells, enclosing a cavity. Within this cavity are so-called **neck-canal cells**, which subsequently disintegrate with the formation of mucilage. At its base the neck becomes expanded to form a **venter**, the wall of which is still only one cell thick. Contained within the cavity of the venter is a single **ovum**, together with a small **ventral canal cell**. The whole structure is borne on a very short stalk, whilst groups of archegonia are enclosed by a thin membrane, known as the **involucre**.

Sporogonium

With the rupture of the apex of the antheridium the mother-cells, embedded in mucilage, are discharged, after which each mother-cell releases its contained spermatozoid. These bodies swim in the moisture,

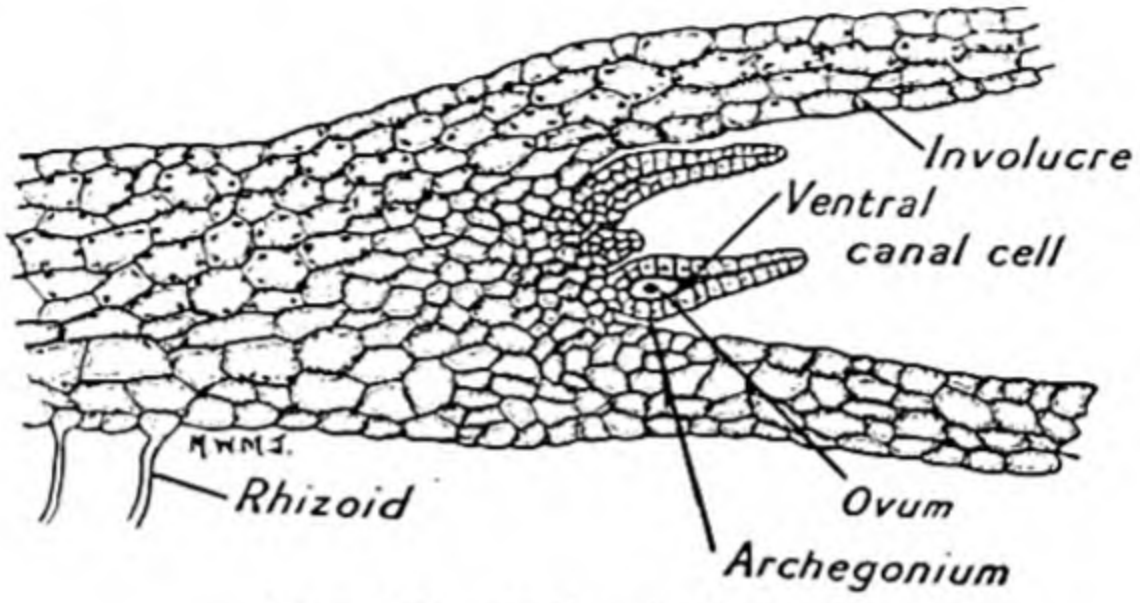


FIG. 146 – *Pellia*. Archegonia.

the presence of which on the surface of the thallus is essential for the completion of the process of fertilisation, and are eventually attracted by chemotaxis (page 454) to the open necks of the archegonia. A single spermatozoid passes down the neck to complete fusion with the ovum in the venter, so that a zygote is formed. This secretes a wall about itself and immediately commences development to form a structure known as a **sporogonium**. The products of early division soon become differentiated into three regions. The **foot** penetrates the thallus, from which it absorbs food. Next above this is the **stalk**, or seta, at first densely packed with starch grains, which disappear during the subsequent elongation, a process resulting in the raising of the sporogonium from the surface of the thallus. At first the sporogonium is retained within the venter, whose wall expands considerably, forming the **calyptra**. The terminal region of the sporogonium is occupied by a **capsule**, which eventually bursts through the calyptra. The wall is some two or three cells thick, and encloses a mass of spore mother-cells, known collectively as the **archesporium**. The cells in *Pellia* are of two kinds. Those of the one type divide each to give rise to four spores: they are therefore true spore mother-cells. The others are at first thin and assist in the conveyance of food to the developing spores. Later they become spirally thickened, forming **elaters**. Owing to this thickening they tend to coil, and thus set up considerable internal pressure within the capsule, the wall of which eventually splits into four valves. Thus the spores are disseminated, giving rise to new plants when they alight on suitable soil. The sporophyte generation is thus parasitic on the gametophyte, a diagnostic feature of this and all higher groups of plants. In the Bryophyta, however, the

parasitism is permanent, whereas in all higher forms it is only temporary. It must, however, be borne in mind that in the Spermaphyta (page 556) the female gametophyte is retained within the sporophyte, whilst it still remains true that the new sporophyte itself commences its development

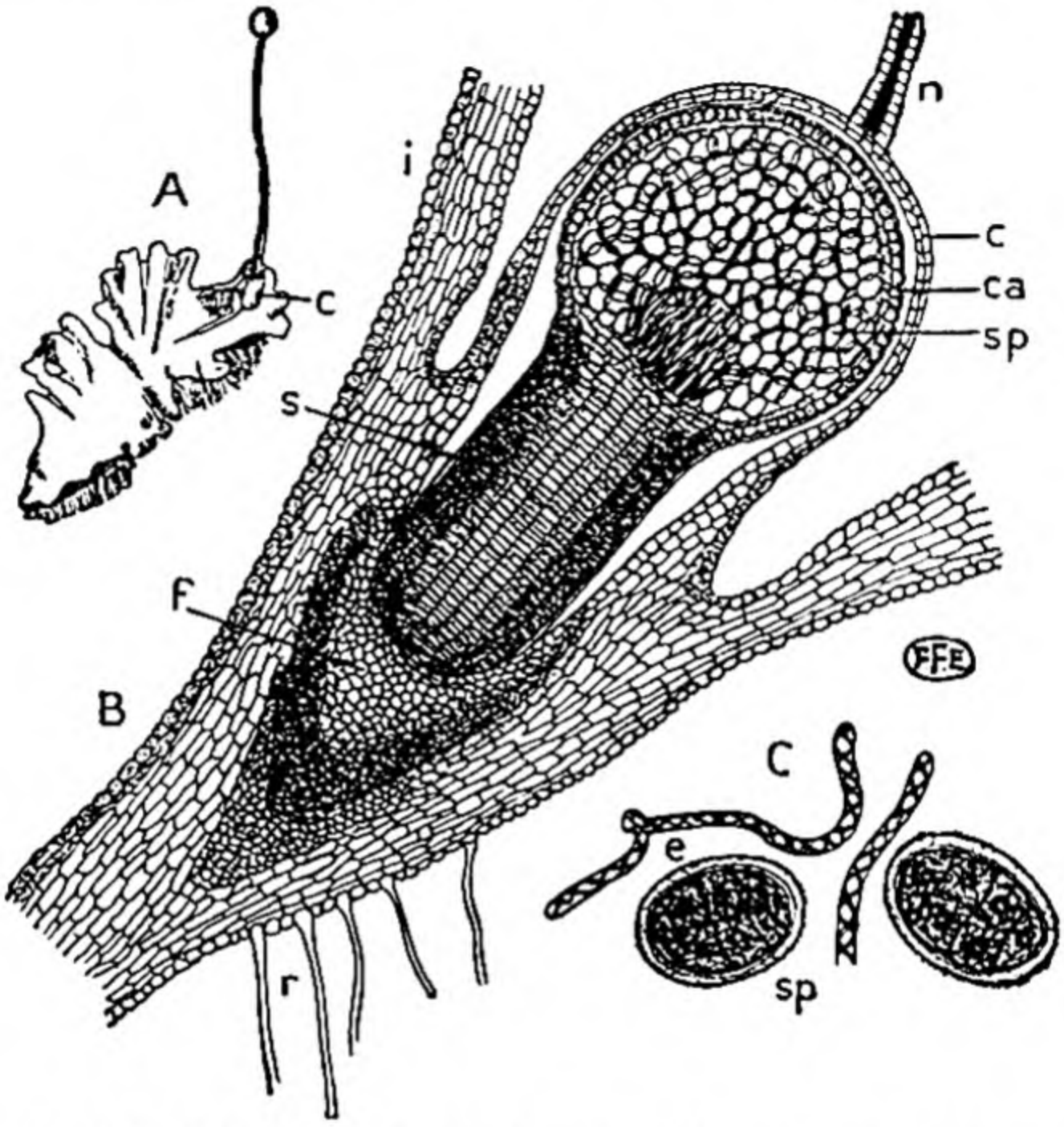


FIG. 147 – *Pellia*, showing the structure of the sporogonium. (From 'Plant Form and Function', by F. E. Fritsch and E. J. Salisbury. Bell.)

A., Small part of a thallus, showing a mature sporogonium, with ruptured calyptra (*c*) at the base (after Leunis). *B.*, Longitudinal section through an almost mature sporogonium, still enclosed within the calyptra (*c*); the elaters are shown as dark lines among the much larger spores. *ca*, wall of capsule; *f*, foot; *i*, involucre; *n*, neck of archegonium; *r*, rhizoid; *s*, seta; *sp*, spore. *C*, A group of spores (*sp*) and elaters (*e*).

within the female gametophyte, on which it is therefore temporarily parasitic.

In conclusion, it should be noted that not all liverworts are of the simple thalloid structure exhibited by *Pellia*. Some of them are, like mosses, foliose (leafy). The leaves differ from those of mosses (see page 220) in that they are usually lobed and often deeply cleft. The stems are often procumbent, bearing two rows of closely packed, sessile leaves;

rhizoids arise from the under surface of the stem. An example is provided by the genus *Cephalozia*.

FUNARIA

Structure

The common cord-moss, *Funaria hygrometrica*, is found principally on walls and rocks. It differs from *Pellia* in that each plant possesses a definite stem, from the base of which project many root-like **rhizoids**. Borne on the stem are small leaves, arranged spirally. Each is oval in shape and bears a distinct mid-rib. The leaves at the base are withered and brownish in colour, whilst those higher up are green. The outer cells

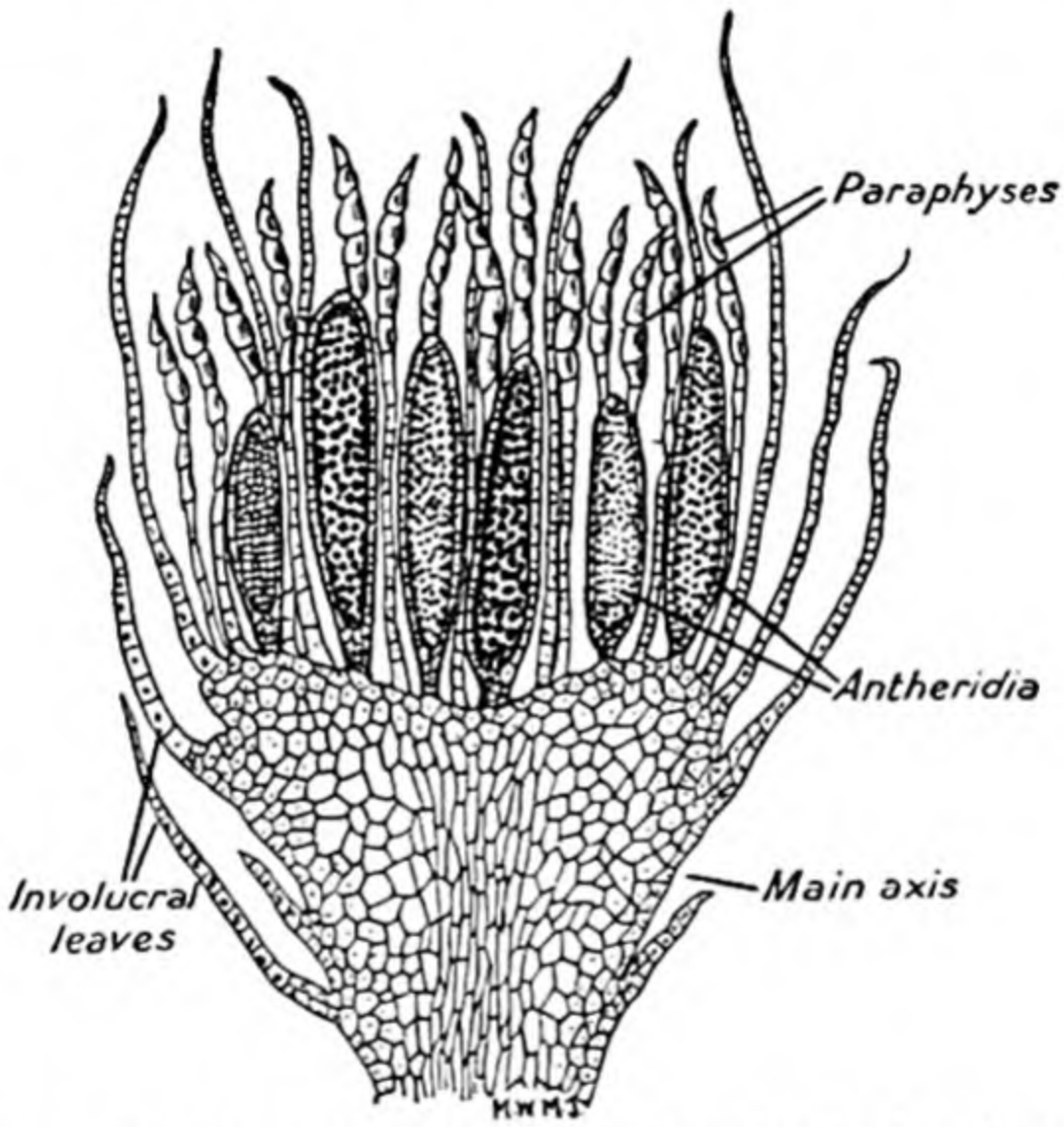


FIG. 148 – *Funaria*. Antheridia in longitudinal section.

of the stem have thickened brown walls in the older part, whilst near the tip they remain green and thin-walled. Within these there is a mass of thin-walled, parenchymatous tissue, containing chloroplasts, whilst the cells in the centre of the stem are small and colourless. Each leaf is but one cell thick and contains many chloroplasts. In the region of the mid-rib the leaf is several cells thick, the central ones being largely concerned in the conduction of water. The rhizoids are branching structures, each composed of cells joined endwise. Those nearer the base of the stem are thick-walled and facilitate anchorage. At the tip of the plant is a cell in the form of an inverted, triangular pyramid, and the cutting off of segments parallel to the surface of this cell results in elongation. Leaves arise

as protuberances from the outer face of some of the segments. Two interesting points about mosses may be noted here. First, they reproduce largely by vegetative means, branching being followed by the dying off of the older parts. Second, they exhibit remarkable powers of recovery after very considerable desiccation.

Reproductive Organs

The reproductive organs, consisting of antheridia and archegonia, are in some cases borne on separate plants, which are consequently described as dioecious, in contrast to the monoecious condition, as in *Funaria*, where both male and female organs occur on different branches of the same plant. The **antheridia** occur at the tip of the plant, being closely crowded and of brownish colour. They are club-shaped, whilst intermingled with them are numerous multicellular hairs, known as **paraphyses**. The wall of each antheridium is but one cell thick and encloses a mass of spermatozoid mother-cells, each of which gives rise to one spermatozoid. The **archegonia**, too, are terminal, and closely resemble those of *Pellia*. Each consists of a **neck** and **venter**, the wall of the former being but one cell thick and enclosing the **neck-canal cells**, which subsequently disintegrate to form a mass of mucilage. The wall of the venter is two cells thick and encloses a single **ovum** and a **ventral canal cell**. Liberated spermatozoids are drawn chemotactically to the neck of an archegonium, and fertilisation occurs as in *Pellia*. The zygote thus formed becomes a **sporogonium**.

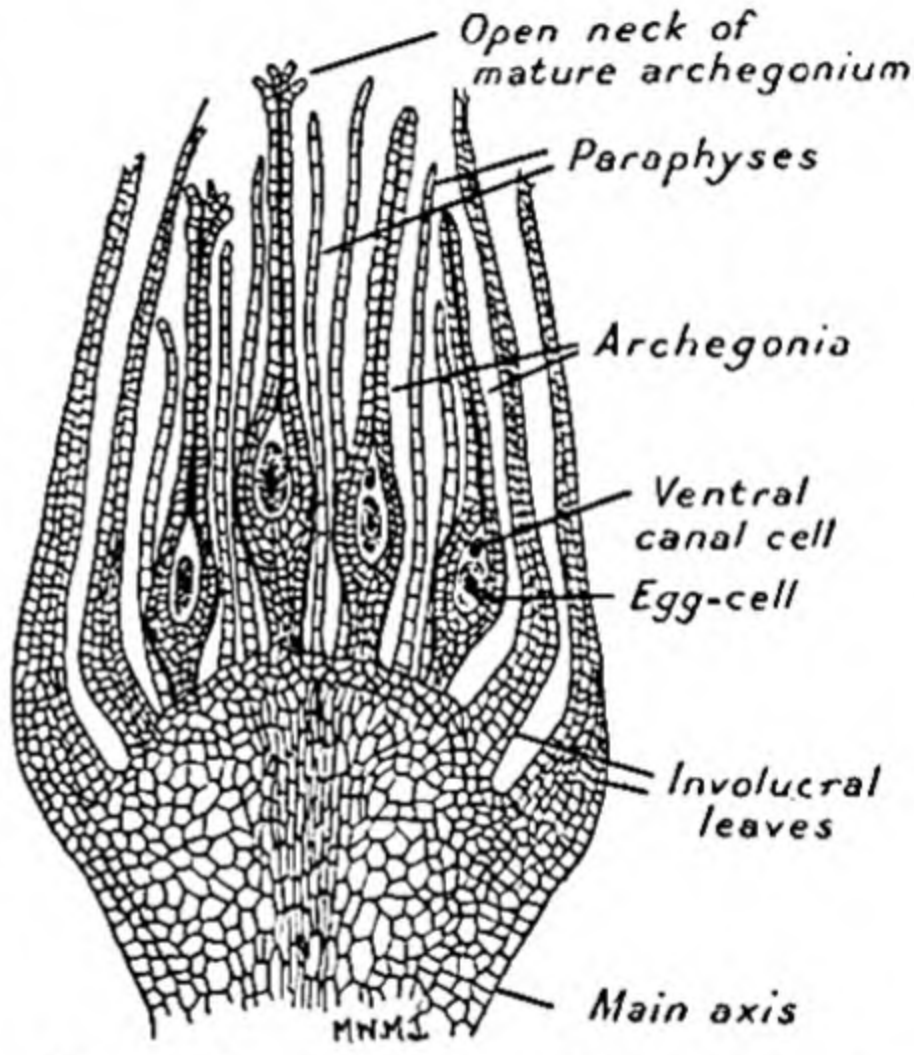


FIG. 149 – *Funaria*. Longitudinal section, showing archegonia.

Sporogonium

The sporogonium of *Funaria* is a comparatively complex structure, and may best be understood by a study of a longitudinal section. At its base it becomes attached to the thallus by a **foot**, serving for the absorption of nutriment. The whole structure is covered distally by an **operculum**, separated from the remainder by a constriction, whilst the whole

sporogonium is enclosed by thick-walled cells, constituting the **epidermis**. This layer is interrupted around the lower margin of the lid by a circular layer of large cells, with irregularly thickened walls, known as the **annulus**. The main axis is occupied by a pillar of thin-walled cells, forming the **columnella**. This is continuous above with the tissue of the lid,

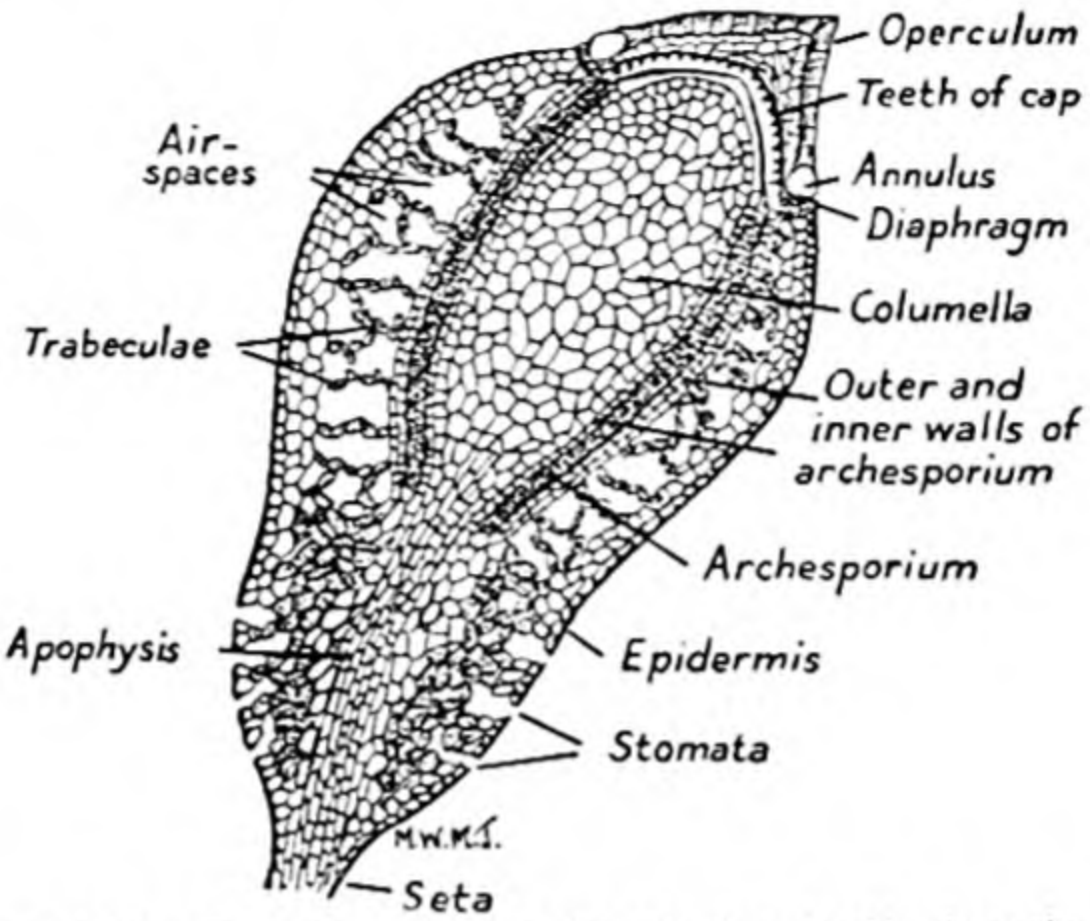


FIG. 150 – *Funaria*. Sporogonium in longitudinal section.

whilst below it is in connexion with the seta by a short column of cells, termed the **apophysis**. Cells arranged in the form of two concentric cylinders surround the columella, and between these two layers of cells is a mass of spore mother-cells, constituting the **archesporium**. Separating the axial pillar of cells from the wall of the capsule is a wide air space, bridged at intervals by single rows of small cells. Just below the lid a perforated disc of thick-walled cells extends from the epidermis to the columella: it is known as the **diaphragm**. From its inner edge there arises a single layer of cells, forming a dome-shaped structure to cover the upper surface of the columella. This layer constitutes the **peristome**, and the outer and inner tangential walls of its component cells are considerably thickened, whilst the radial (*i.e.*, vertical) walls remain thin. As the capsule matures all the thin-walled cells disintegrate, leaving only the epidermis, the diaphragm and the thickened walls of the peristome. Dehiscence occurs at the annulus and the operculum breaks away. The partial disintegration of the peristomial cells results in this layer's assuming the form of a double series of tooth-like structures, whose disposition depends upon the moisture-content of the atmosphere. Only when the air is dry will they bend outwards to permit the escape of spores, four of which have been formed by the meiotic divisions of each spore mother-cell. In damp conditions a dome is reconstituted by the arching

inwards of the peristome teeth. Actual dispersal occurs on the catapult principle, the elasticity of the seta being an important factor.

Thus, as in *Pellia*, there are two generations in the life-history, and the sporophyte is again parasitic on the gametophyte. The germination of the spore to produce eventually a new gametophyte plant is important. From the spore there emanates a short, colourless structure, known as the **protonema**. It branches profusely, whilst chloroplasts appear in some of the branches, others penetrating the soil as colourless rhizoids. A tetrahedral cell soon becomes distinguishable at the apex of one of the

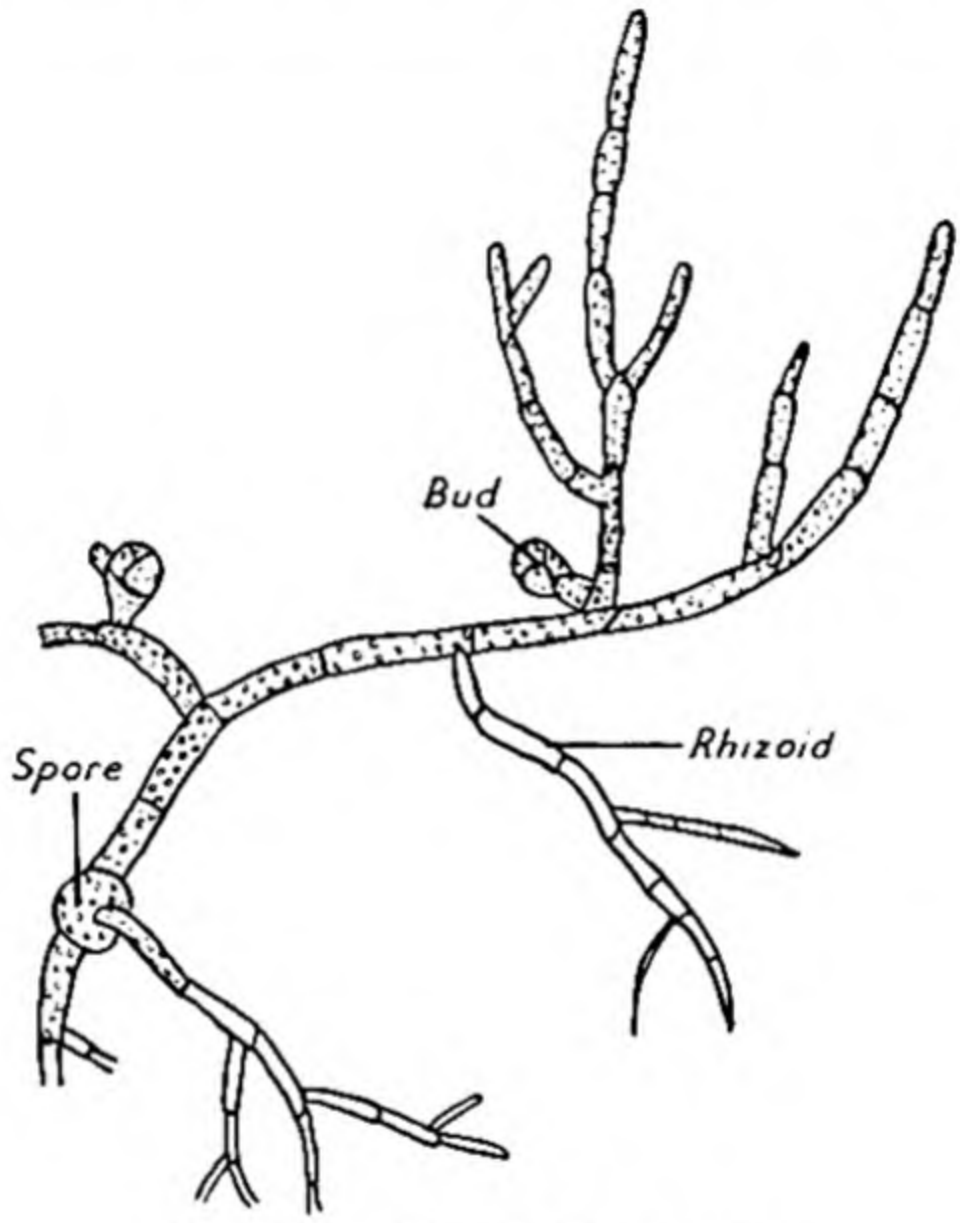


FIG. 151 – *Funaria*. Protonema.

branches, and this is the growing point of the new plant. Prior to its formation considerable vegetative reproduction by the protonema may be effected by the detachment of some of the branches.

DRYOPTERIS (= NEPHRODIUM)

Dryopteris, the common shield fern, belongs to the class **Pteridophyta.** In principle the life-history of members of this class resembles that of the Bryophyta in that the sporophyte generation is parasitic on a thalloid gametophyte; but this condition persists for only a short time in the Pteridophyta, after which the sporophyte grows up into a comparatively large, independent generation. The moss plant is a gametophyte and

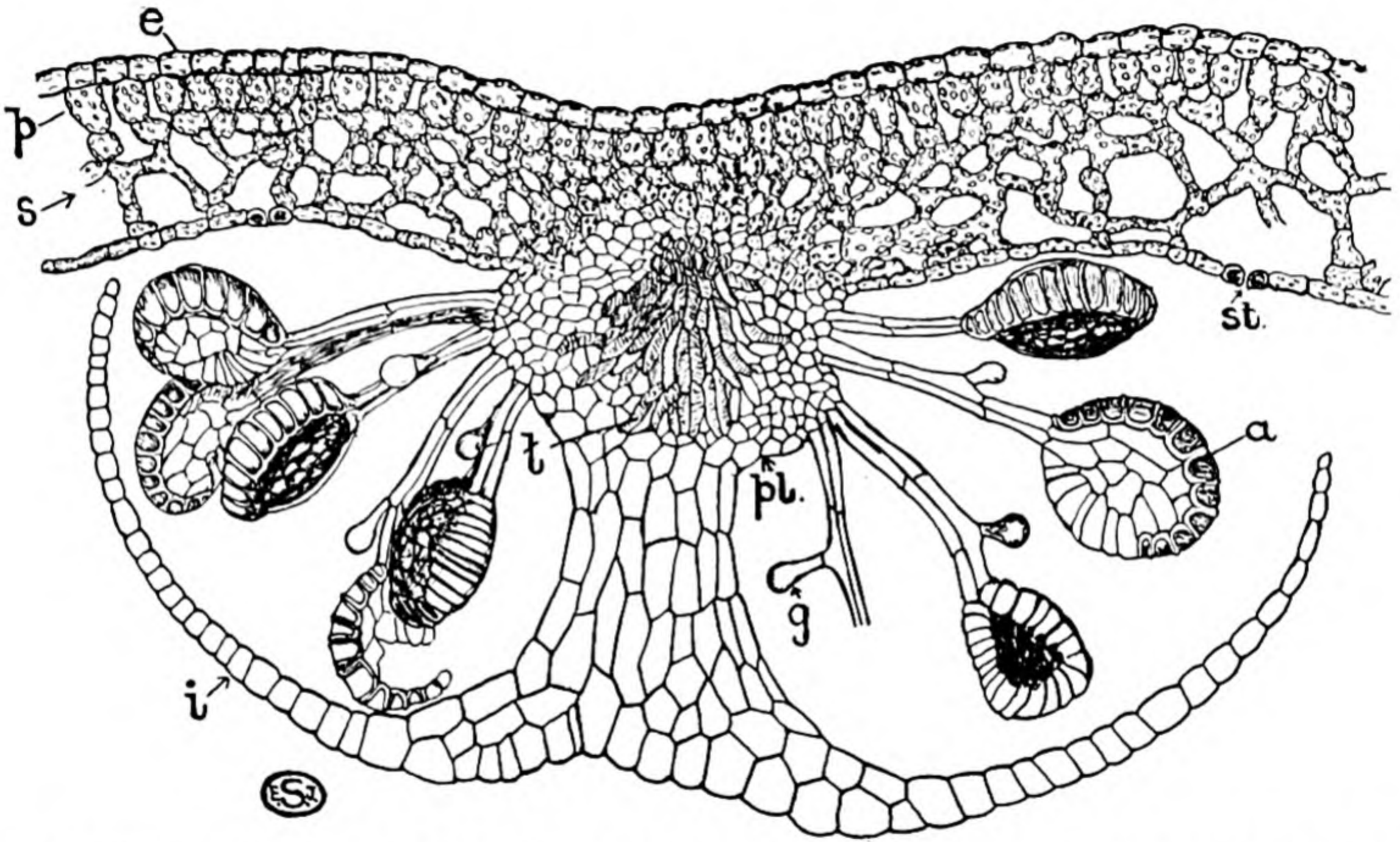


FIG. 152 – Transverse section of a pinna, passing through a sorus, of the Male Fern (*Nephrodium filix-mas*). (From 'Plant Form and Function', by F. E. Fritsch and E. J. Salisbury. Bell.)
It shows the indusium (*i*), the placenta (*pl*), and sporangia in various positions and stages of development. *a.*,annulus; *e.*, epidermis; *g.*, gland on sporangial stalk; *p.*, palisade tissue; *s.*, spongy tissue; *st.*, stoma; *t.*, tracheids.

represents the most highly developed condition of this generation in the whole plant-kingdom. The fern plant, on the other hand, is a sporophyte. This matter is considered further in Chapter 32. Further, the Pteridophyta are characterised by the presence of specialised roots and conducting tissue.

Structure

The conspicuous plant is the sporophyte generation. It is clearly divisible into root and shoot, the latter consisting of the whole aerial portion of the plant, as well as a part underground from which adventitious roots (page 289) arise. The large, expanded structures apparent in the shoot are termed **fronds**. They are considerably subdivided, the individual branches being known as **pinnae**. On the under-surface of some of the pinnae are small, brown masses, known as **sori**, whose detailed structure will be considered later.

ROOT. As pointed out above the roots of the fern are adventitious. The root is best studied in transverse section. It is very similar in structure to that of a Dicotyledon (Chapter 17). Borne on the outermost layer are numerous **root-hairs**, whilst within this layer is a many-celled **cortex**, bordered on its inner side by an **endodermis**. Within the endodermis is a single layer of cells, constituting the **pericycle**. Contained in the central cylinder of the root are two bundles of **xylem**, alternating with two bundles of **phloem**. The root may therefore be described as **diarch**.

STEM. The arrangement of tissue in the stem is similar to that in the root, but the vascular strands, unlike those of flowering plants, branch and unite to form a network. Thus in transverse section they present an irregular appearance.

FROND. The frond is bordered by an upper and a lower **epidermis**, the latter being perforated by **stomata** (page 260). Both upper and lower epidermis contain chlorophyll. The tissue between these limiting layers, known as the **mesophyll**, consists of irregularly-arranged, parenchymatous cells, rather more closely packed towards the upper surface, as shown in Fig. 152. The row of regular cells immediately below the upper epidermis is termed the **palisade layer**. The cells of the mesophyll contain chloroplasts.

Sporangia

Most important of the structure of the frond is that of the **sori**. Each consists of a mass of sporangia covered by an umbrella-like **indusium**. The sporangia arise from a stalk, or **placenta**, a structure corresponding in position to the handle of the umbrella. Each sporangium is a biconvex structure. Its margin is formed by a layer of cells, known as the **annulus**, reaching from the base on one side to about half-way down the opposite side, passing over the apex. The inner and lateral walls of the cells of the annulus are considerably thickened. Completing the margin are thin-

walled cells, constituting the **stomium.** The **capsule** of the sporangium in its early development is divisible into three layers. The outermost is the wall, one cell thick, lined by a nutritive layer, termed the **tapetum.** In the centre is at first a single cell, known as the **archesporium.** This latter divides to give rise to a mass of spore mother-cells, each of which produces four spores. During this process the tapetum disintegrates to provide the requisite nourishment. As the sporangia ripen the indusium

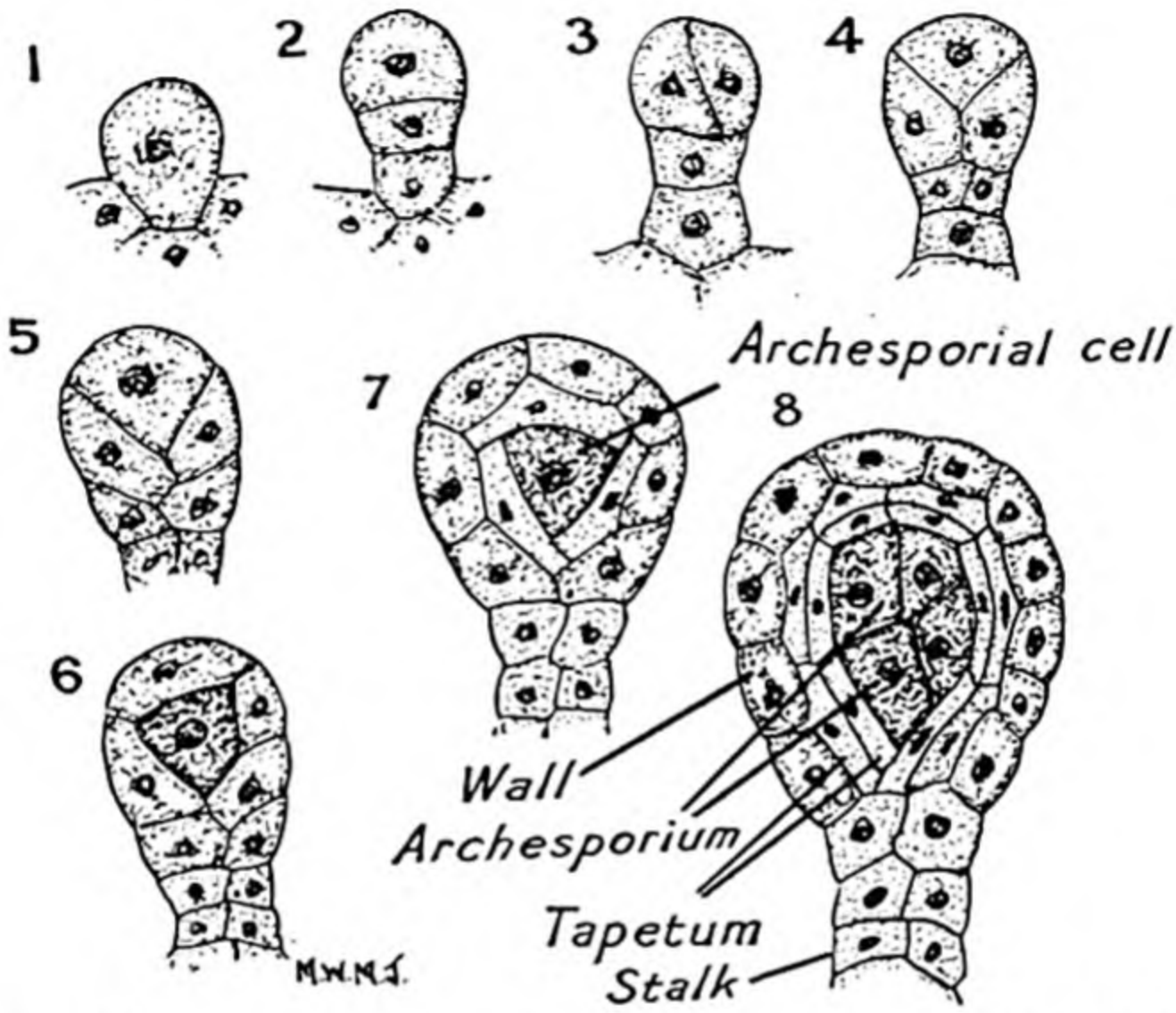


FIG. 153 – *Dryopteris*. Stages in the development of the sporangium.

withers. The annulus plays an important part in the dehiscence of the sporangium. Some of the water of the sap contained in the cells of this layer is lost by evaporation, and the cohesion between the remaining water and the cell-walls draws inwards the thin outer and radial walls. The net result is a shortening of the annulus, and eventually the stomium ruptures. The tear is continued across the cells of the sporangium, dividing it roughly into upper and lower halves. The annulus still continues its contraction and is now free to bend backwards, carrying with it some of the contents of the sporangium, including spores. Eventually the loss of water from the cells becomes so great that the cohesion between water and cell-walls is overcome. An air-bubble appears in each cell, which now recovers its original shape and size. In consequence the annulus as a whole returns with some violence to its former position, thus flinging out many of the spores contained within the capsule, and their dispersal is completed by wind.

Prothallus

The spore germinates in water. Its outer coat ruptures and a colourless process appears. This becomes a root-hair, whilst the remainder of the living material becomes a single filament, at the edge of which a specialised, apical cell may soon be distinguished by its commencing to produce lateral cells. Eventually the structure comes to be known as a **prothallus**, and is heart-shaped, with the growing-point situated in the depression. It is but one cell thick, and is composed of parenchymatous

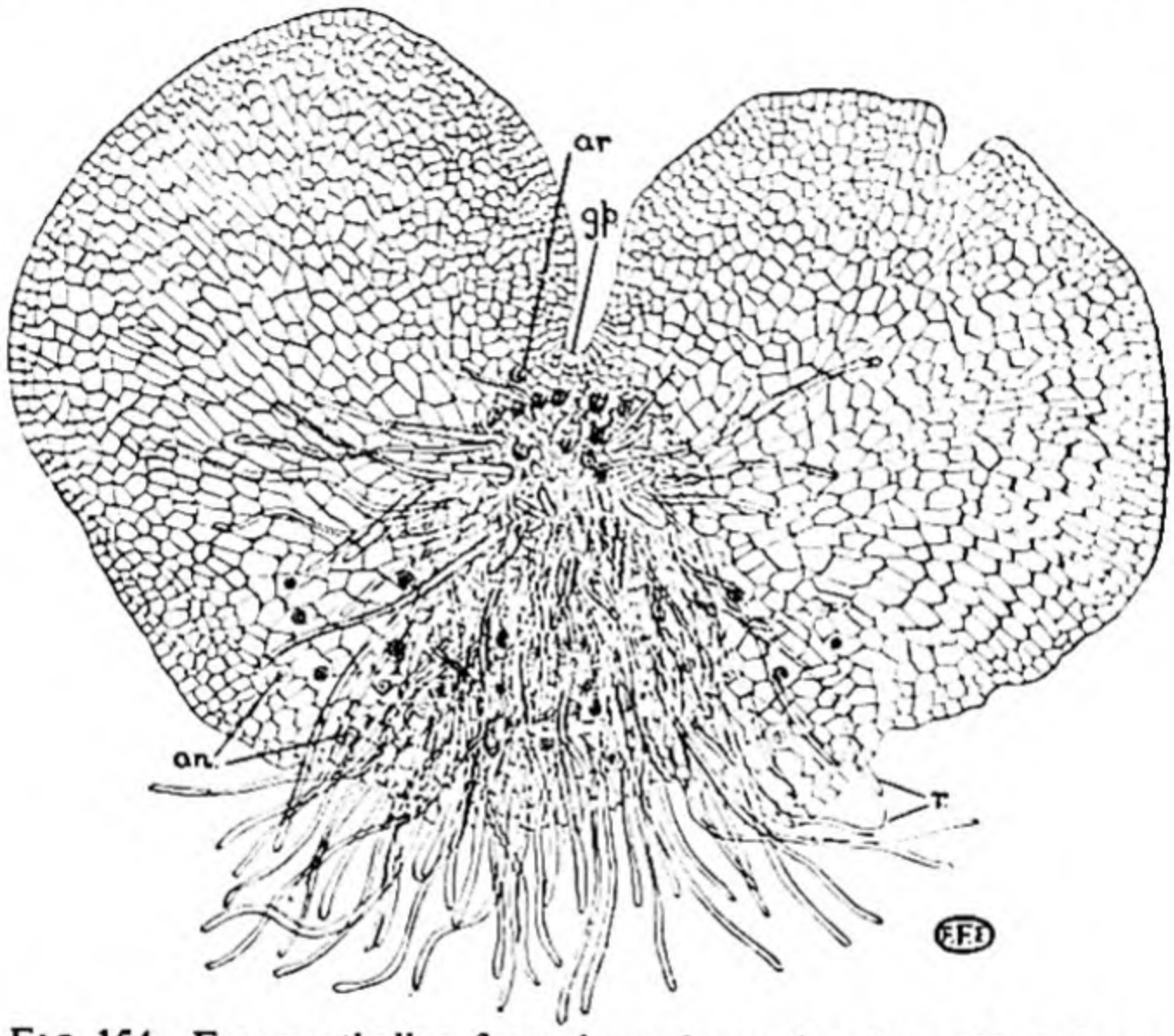


FIG. 154 – Fern prothallus, from the under-surface (magnified about twenty times). (From 'Plant Form and Function', by F. E. Fritsch and E. J. Salisbury. Bell.)
A considerable number of antheridia (*an.*) are seen, on the older part, and the projecting necks of twelve archegonia (*ar*), in the region of the cushion, from which also arise numerous rhizoids (*r.*). *g.p.*, meristem.

cells containing chloroplasts. In the centre it is many cells thick, forming the so-called **cushion**, from the under-surface of which arise numerous rhizoids. This structure corresponds to the thallus of *Pellia* and *Funaria*, and like it bears sexual organs. It is, in fact, the gametophyte generation.

REPRODUCTIVE ORGANS. Both antheridia and archegonia normally occur on the same prothallus, being visible on the under surface. **Archegonia** are clustered in the region of the cushion, and closely resemble those of the Bryophyta. They are partly embedded in the tissue of the cushion, whilst at the base the curved **neck** is expanded to form a **venter**, containing a single egg-cell and a ventral canal cell. At maturity mucilage

is exuded from the open neck, containing traces of malic acid. This exerts a positive chemotaxis on the spermatozoids liberated from the antheridium. **Antheridia** are found scattered singly towards the margin of the prothallus. Each is an almost spherical cavity, containing numerous spermatozoid mother-cells. The wall consists of two superposed ring-shaped cells, whilst the cavity is at first closed by a dome-shaped cap. Dehiscence is effected by the removal of the cap, the spermatozoids being liberated. Each is a somewhat coiled body, bearing a bunch of flagella

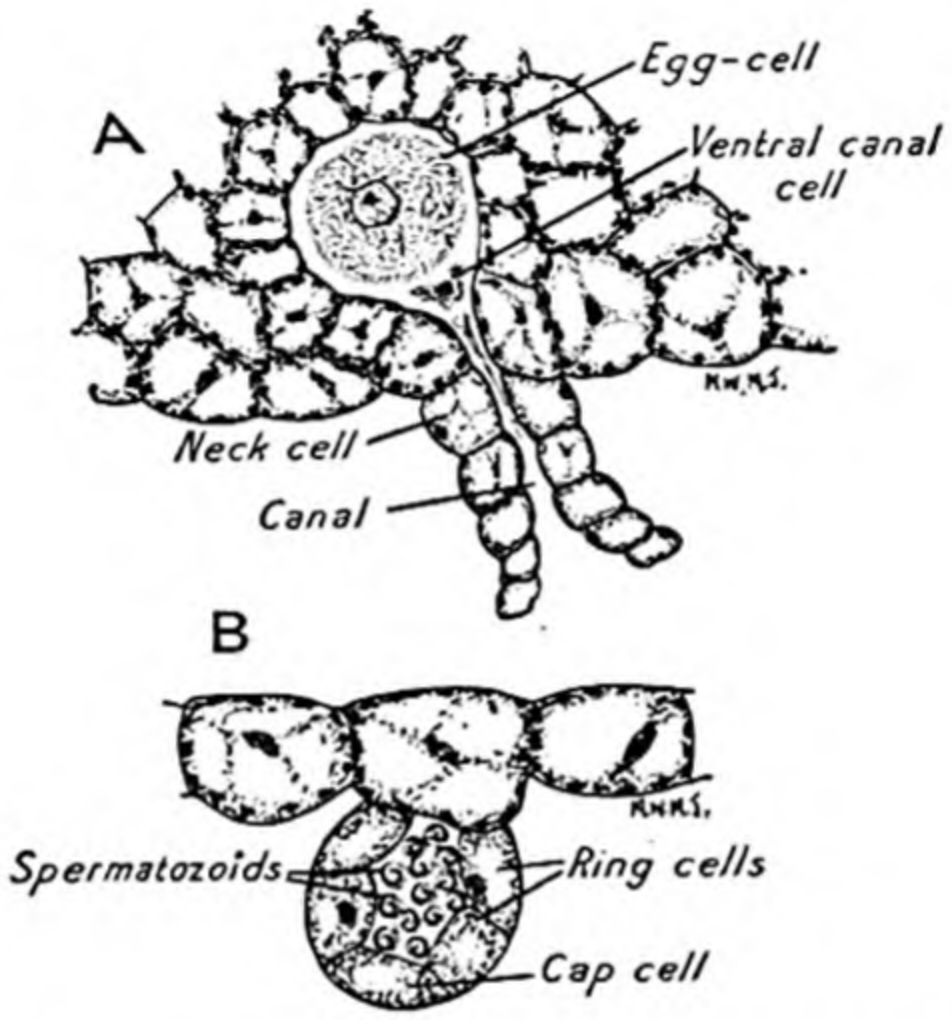


FIG. 155 – *Dryopteris*. *A*, An archegonium in vertical section; *B*, An antheridium in vertical section.

at one end and swimming in the film of moisture retained by surface tension between the prothallus and the soil. Attracted chemotactically by the malic acid from the archegonia, a spermatozoid eventually fertilises an egg-cell, forming a zygote.

Development of Sporophyte

The zygote commences to develop at once, dividing first three times to form a mass of eight small cells. From these all the various regions of the new sporophyte are derived, and this structure remains for some time in nutritive connexion with the gametophyte by means of a foot. Presently the new sporophyte develops a root of its own, piercing the prothallus to reach the soil. This primary root is soon lost and is replaced by adventitious roots, given off from the base of the stem. The remains of the prothallus then perish.

Thus in the fern the sporophyte is the conspicuous generation, an

advance on the condition in the Bryophyta. It is this generation which has become so highly developed in adaptation for the colonisation of land.

PRACTICAL WORK

Pellia

Cut transverse sections of the thallus. Draw. These should be taken parallel to the long axis, and some of them will pass through antheridia, and possibly the growing point. These should be studied and drawn very carefully. Examine and draw sporogonia, including the contents of the capsule.

Funaria

Examine a complete plant with a hand lens, identifying the various parts. A plant bearing a sporogonium must be examined and drawn.

Cut transverse sections of stem and leaf. Draw.

Cut sections passing through antheridia, and others through archegonia. Examine and draw.

Cut longitudinal sections of sporogonia until one is discovered at the stage of development shown in Fig. 150. Draw and label fully.

Dryopteris

Examine an entire plant, noting carefully the arrangement and external structure of the various parts. Sketch it.

Examine carefully the under surface of a frond, bearing the sori. Draw a single pinna to show their positions.

Boil the short stem in dilute hydrochloric acid. The remainder of the tissues may then easily be removed to expose the conducting elements.

Examine a vertical section through a sorus, identifying the parts with the aid of Fig. 152. Draw. Examine a single sporangium under high power. Draw representative portions.

Examine a prothallus, numbers of which may generally be found growing near the fully-formed ferns. Examine with the low power the under surface of the prothallus, noting the positions of the antheridia and archegonia. Mark these on a sketch.

Examine prepared transverse sections of the prothallus, noting the details of the antheridia and archegonia, as shown in Figs. 155, A and B.

If ripe sporangia of *Dryopteris* or other fern are available, scrape off a few and mount in glycerol. The dehiscence of the sporangium and expulsion of the spores may then be observed, since the glycerol removes water from the annulus cells.

CHAPTER 13

Pinus

Pinus sylvestris, the Scots Pine, belongs to the group **Gymnospermae**. Members of this group give rise to seeds, but these seeds are borne on open scales. The only class of this group for present consideration is the **Coniferae**, characterised by the possession of cones. The interest of the plant lies mainly in its reproductive activities, but a short description of its structure will first be given.

Structure

Pinus, occurring commonly in northerly latitudes, takes the form of a large tree with a straight, thick trunk. The carpellate cones (see later) are borne annually at the tips of the branches, whilst the staminate cones are spirally arranged. Branches develop in whorls, arising each in the axil of a scale leaf at the end of a year's growth. As well as these *long* shoots (of unlimited growth), *dwarf* shoots (of limited growth) are formed. Upon the long shoots only do scale leaves occur, whilst the characteristic green 'needles' are found only on the dwarf shoots. The latter shoots, with their clusters of attached leaves, are termed *spurs*, and ultimate leaf-fall is achieved by the shedding of the complete dwarf shoots.

ROOT. The root is very like that of an Angiosperm, described fully in

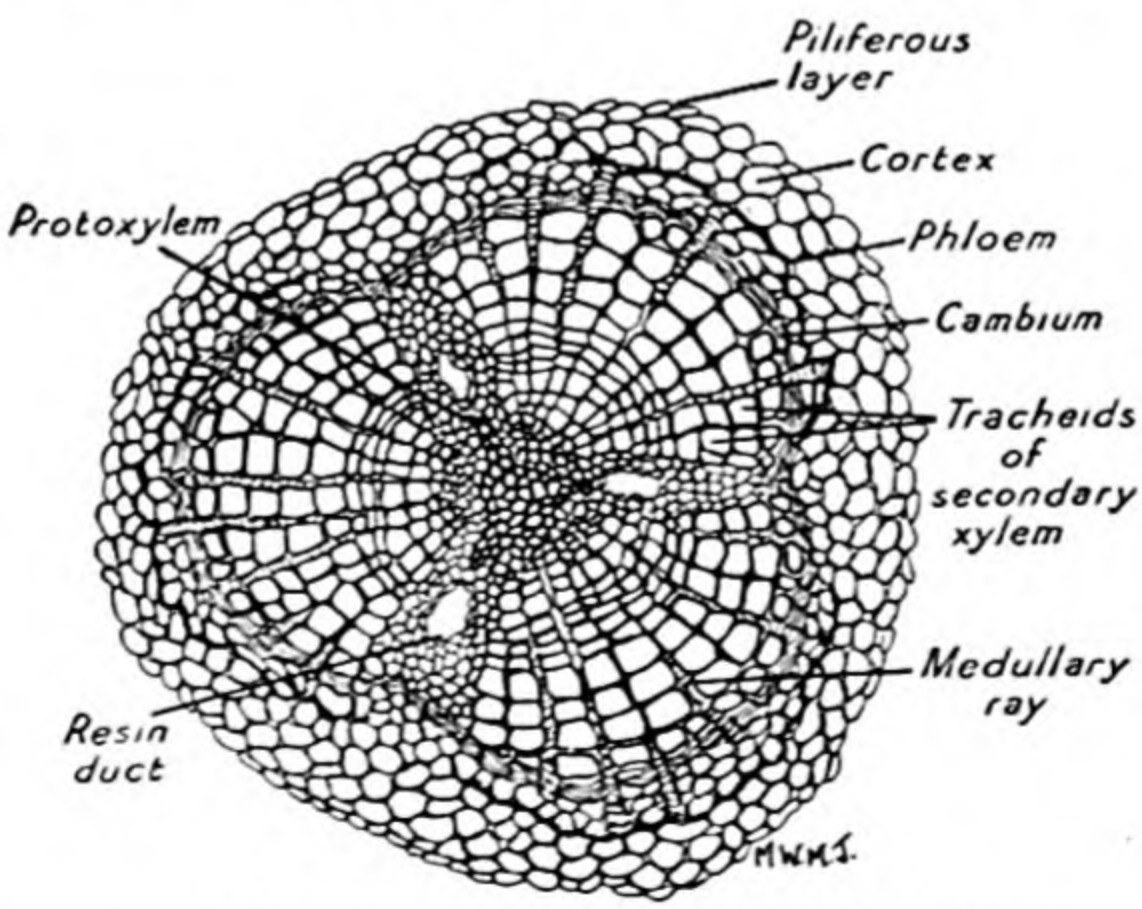


FIG. 156 – *Pinus*. Transverse section of the root.

Chapter 17. The bundles of **primary xylem** become continuous across the centre of the root, whilst secondary thickening results in the formation of a mass of **secondary xylem**, clearly distinguishable into winter and summer wood. It is traversed by numerous **medullary rays** and penetrated by many **resin-ducts**. A cork cambium, or **phellogen**, arises outside the pericycle, giving rise to **cork** on its outer side. The growing-point is

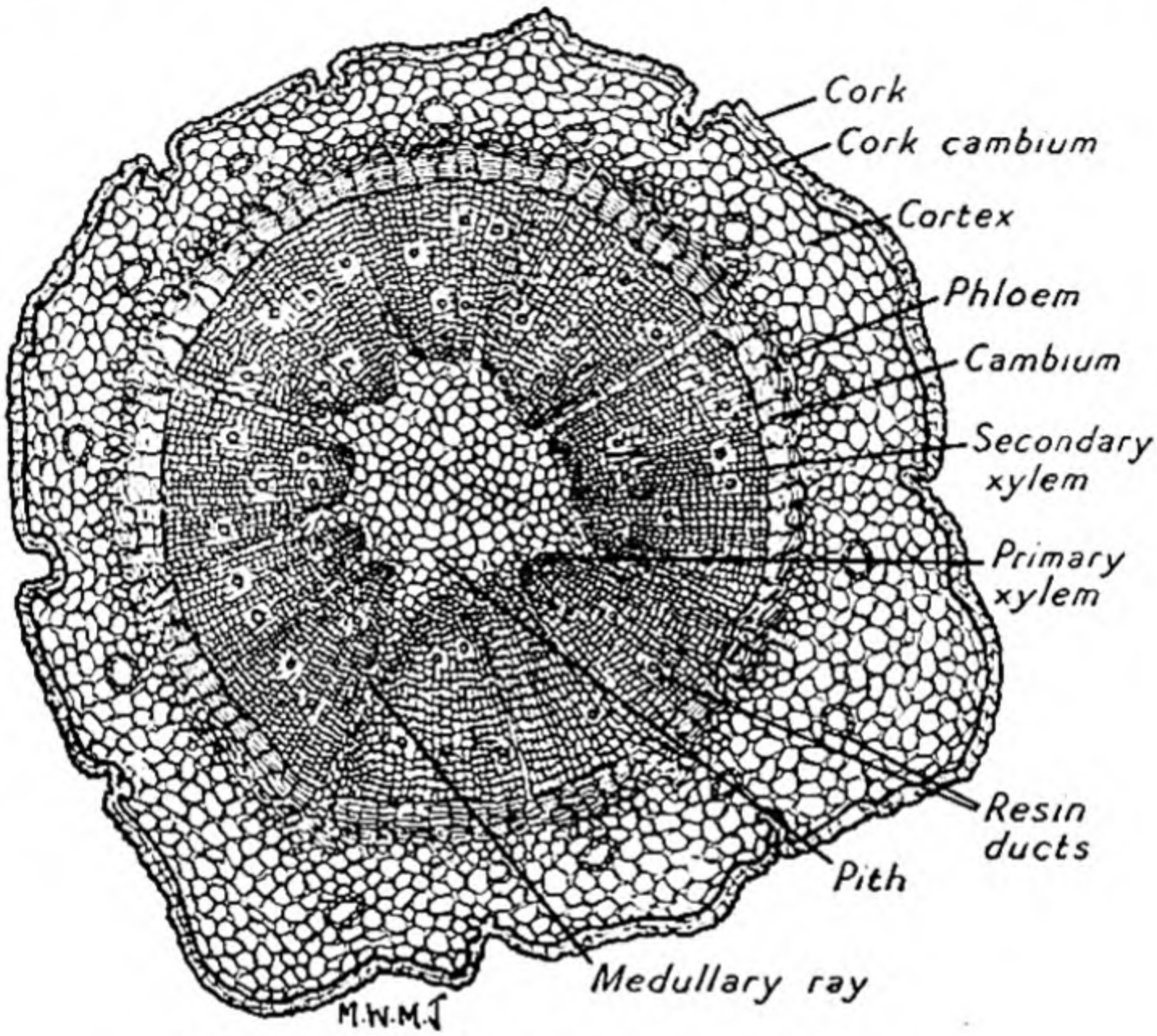


FIG. 157 – *Pinus*. Transverse section of the stem.

divisible into two regions (like that of Angiospermae), the outer layer giving rise to the root-cap and early superficial layers.

STEM. The stem also is similar to that found in the Angiospermae, but as secondary thickening occurs certain points of difference become apparent. The medullary rays are more regularly arranged in the secondary xylem, which itself consists entirely of **tracheids** (page 339). The absence of vessels from the xylem causes the grain of the wood (known as deal) to be much more uniform than that of the oak, for example. The sieve tubes of the phloem have sieve plates (page 339) on their radial walls, whilst no companion cells are present. Annual rings are found as in Angiospermae, as well as a layer of cork from a cork cambium.

LEAF. The leaves, or needles, are flattened on the upper surface and convex beneath. The whole is enclosed in a cuticularised **epidermis,**

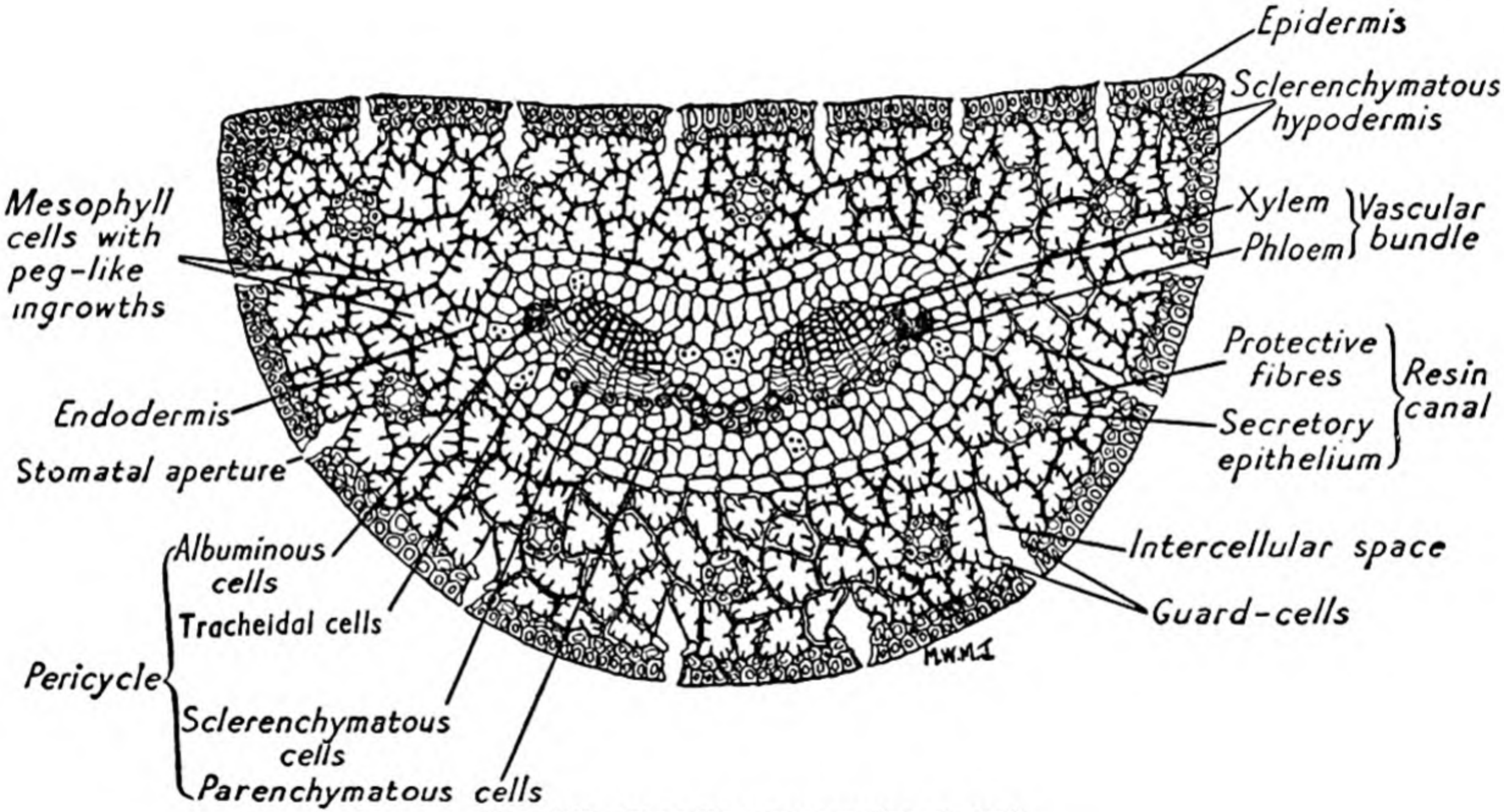


FIG. 158 – *Pinus*. Transverse section of a leaf.

whilst the guard-cells of the stomata are sunk beneath the surface. Beneath this layer is a sclerenchymatous **hypodermis**, several cells in thickness. Within is the assimilating tissue, containing numerous chloroplasts. This layer is quite compact, but air-spaces are introduced by the invagination of the walls of some of the cells, whilst the tissues are arranged in transverse lamellae, thus enclosing additional air-spaces. Running in this tissue are resin-ducts. Each is lined by thin-walled cells

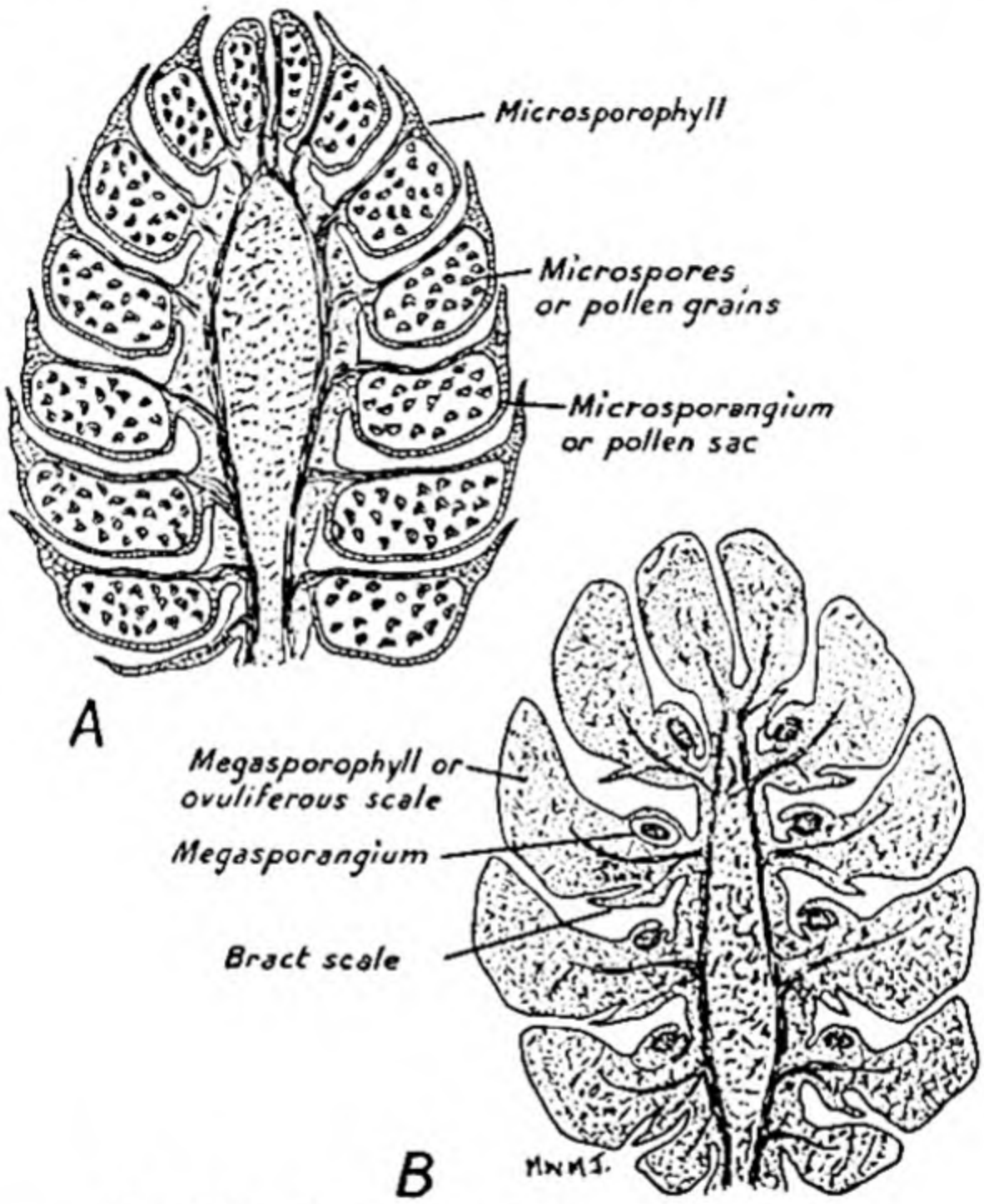


FIG. 159 – *Pinus*. Cones in longitudinal section.
A., Staminate cone; *B*., Carpellate cone.

and enclosed by sclerenchyma. The central cylinder is bordered by an **endodermis**, within which is the **pericycle**. This is differentiated into a number of types of cell of characteristic disposition. The bulk of it is parenchymatous, some of the cells being rich in protein and starch content and known as **albuminous cells**. A further portion of the pericycle assumes the form of **fibres** surrounding the vascular bundles. The albuminous cells, together with a number of pitted cells, constitute the **transfusion tissue**. There are but two bundles in a leaf, with the **xylem** towards the upper and the **phloem** towards the lower surface.

Cones

These are of two kinds. The male, or **staminate**, cones are so called on account of their correspondence to the stamens of Angiospermae, whilst the **carpellate** cones are comparable with the pistil, though they do not enclose the ovules.

(A) STAMINATE CONES. The staminate cone is essentially a collection of scale-like structures, known as **microsporophylls**, spirally arranged about an axial stem. On the under-surface of each occur two pollen sacs,

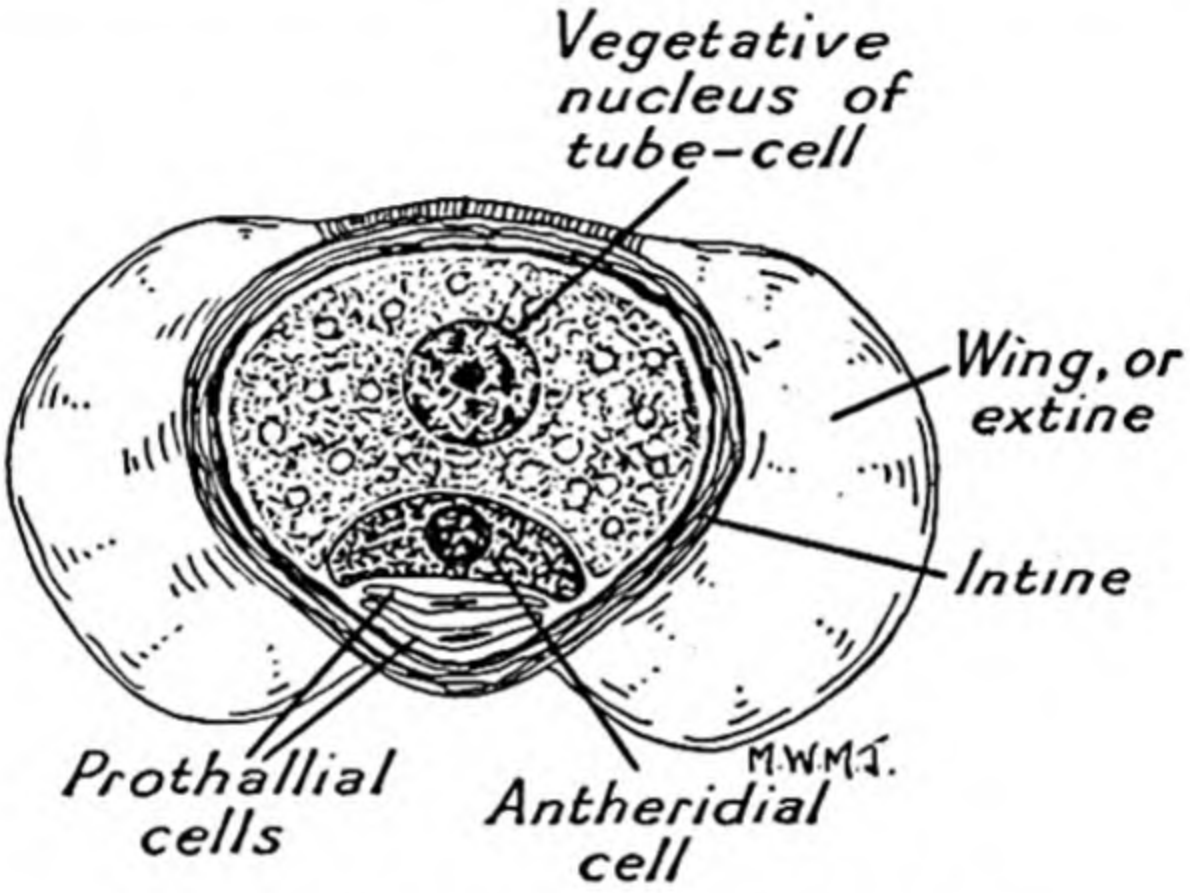


FIG. 160 – *Pinus*. Mature pollen grain.

or **microsporangia**, each of which contains many pollen mother-cells. Each of these divides to form the customary four pollen grains, or **microspores**. When ripe the pollen grain bears two lateral, expanded processes, facilitating distribution by wind.

(B) CARPELLATE CONES. Each consists, like the staminate cone, of a number of spirally-arranged scales, known as **megasporophylls**, on a central axis, though a few of the scales at the base are sterile. Each megasporophyll is essentially double, as shown in Fig. 159B. It consists of a basal portion, known as the **bract scale**, bearing an expanded **ovuliferous scale**. This carries on its upper surface two **megasporangia**, or ovules.

Pollination and Fertilisation

A peculiarity of the processes of pollination and fertilisation in *Pinus* is the interval of some twelve months between the two. At the time of pollination the microspores have already become considerably differentiated. A single, well-defined cell has become distinguishable as the

antheridial cell, whilst pressed against the surface are two small cells, constituting the **prothallus**. The remainder of the spore is occupied by a large **vegetative cell**. This condition is shown in Fig. 160.

The ovules, too, have undergone a certain degree of development prior to pollination. Each is enclosed within a single, thick **integument**, interrupted at the end directed towards the axis of the cone by a pore, known as the **micropyle**. Within the integument is a mass of tissue, constituting the **nucellus**. At the micropylar end of the nucellus, just below the surface, a single cell enlarges to form the **archesporium**. This divides to form a number of cells, one of which is the **archesporial cell**, well embedded in the nucellus. This cell now divides twice by meiosis (page 316), resulting in the formation of a row of four potential **megaspores**, each with the

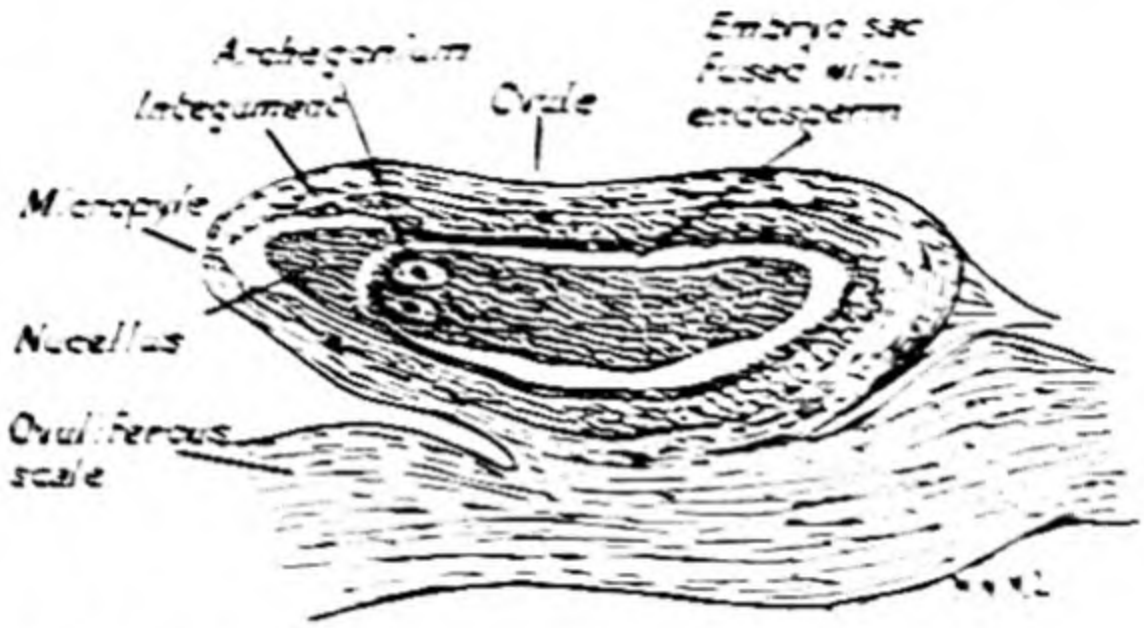


FIG. 161 – *Pinus*. A mature ovule in transverse section.

haploid number of chromosomes (page 313). Only the innermost one becomes functional and is often termed the **embryo sac**. The nucellus and its contained embryo sac constitute the **megasporangium**.

With the micro- and mega-spores in the condition described above pollination occurs. The scales of the female cone are forced wide apart by the elongation of the axis. Pollen grains pass amongst these and are entrapped by a mucilaginous secretion exuding from the micropyles. As this fluid dries the pollen grains are drawn inwards, whilst the enlargement of the scales results in their becoming completely imprisoned.

Pollination thus completed, the microspore continues development for a while. The vegetative cell becomes extended to form a **pollen tube** projecting down the micropyle, whilst the antheridial cell divides to form an upper and lower product, the lower one eventually dividing again to form two **male cells**. At this point the development of the pollen grain is arrested for twelve months. At the same time as the pollen tube has been extending, differentiation within the ovule has continued. Within the embryo sac rapid cell division takes place to form a mass of thin-walled parenchymatous tissue (page 321), which largely displaces the nucellus, now represented by little more than a cap at the micropylar

end (Fig. 161). This mass of parenchymatous tissue constitutes the **female prothallus**. Within this arise three **archegonia** at the micropylar end. Each consists of a single, large ovum, surrounded by a specialised layer of the cells of the prothallus, whilst a short, inconspicuous **neck** projects from the micropylar end. Immediately previous to fertilisation a **ventral canal-cell** is cut off at the base of the neck.

Just prior to fertilisation the growth of the pollen tube is continued, penetrating the nucellus to reach the neck of an archegonium. Meanwhile the two male cells have passed along the pollen tube, and one of them usually disappears. The other, on reaching the archegonium, fuses with the nucleus of the ovum.

Formation of Seeds

The fertilised egg, or **oöspore**, becomes enclosed within a thin membrane, and immediately a double division of its nucleus results in the formation of four nuclei, which take up a position at the end away from the micropyle. As a result of further division and the formation of separating walls several tiers are formed, each composed of some four cells. The tier farthest away from the microphyle gives rise to the embryo plant, whilst the remainder elongate to form a **suspensor**, pushing the embryo farther into the tissue of the prothallus. Soon a **plumule**, surrounded by a large number of **cotyledons**, becomes differentiated, whilst adjacent to the suspensor a **radicle** arises. The integument of the ovule hardens to form the seed-coat, or **testa**, whilst that part of the female prothallus which persists in the mature seed constitutes the **endosperm**. The micropyle remains as a minute pore in the testa, and immediately within it lies the radicle, ready for subsequent emergence. The ripe seeds are discharged from the female cones in the third year of the latter's life. This is effected by the opening of the cones, whilst each seed bears a winged process, derived from a fragment of the ovuliferous scale of the megasporophyll, to facilitate dispersal by wind.

Summary of Life-history

The pine tree itself is the sporophyte generation, giving rise to the two sorts of prothallus mentioned (male and female), each of which corresponds to the gametophyte of lower forms, though the sexes are separate. This condition is discussed further in Chapter 32.

Germination

The method of germination is epigeal, almost identical with that described for a castor oil seed on page 550.

The general significance of the various features of the life history of *Pinus* is described in Chapter 32.

PRACTICAL WORK

If available, examine a branch of *Pinus*. Note the arrangement of the cones. Look for carpellate cones of various ages, namely: (*a*) after pollination; (*b*) after fertilisation; (*c*) after dispersal of seeds. Examine staminate cones. Sketch.

Examine prepared sections of the young and older stem and root, and of the leaf. Compare with the figures given in the text. Draw.

Examine prepared longitudinal sections of staminate and carpellate cones. Draw. Sections may be cut by the student if the cones are previously preserved for some time in alcohol.

CHAPTER 14

Angiospermae. The Stem

The final subdivision of the plant-kingdom is the **Angiospermae**, which, together with the Gymnospermae, constitute the **Spermaphyta** (Seed Plants). Members of this class are characterised by the formation of **ovules** within a closed cavity, known as an **ovary**, so that pollen grains cannot come into direct contact with the nucellus, but are deposited on a part of the pistil (*q.v.*) known as the **stigma**, from which the greatly elongated pollen tube passes through a tubular style eventually to reach the ovary. The stamens (*q.v.*) are each differentiated into stalk and head, whilst surrounding these essential organs are whorls of sterile structures, known collectively as the **perianth** and usually composed separately of sepals and petals. Each region of the plant will be considered in turn, the stem being the subject of the present chapter.

External Form

The stem, bearing leaves and flowers, is that part of the plant which arises from the plumule of the seed (Chapter 31). The positions at which leaves are attached are known as **nodes** and the spaces between them as **internodes**. Elongation and the formation of new branches is effected primarily by buds, but as these are composed principally of folded leaves they will be considered in Chapter 15. The form of the shoot varies according to conditions under which growth is taking place. From this point of view it may be subdivided into two main types – aerial and subterranean.

Aerial Shoots

According to form and texture these are herbaceous, shrubby or woody. The material of a herbaceous stem remains soft, whilst that of a shrubby or woody stem becomes considerably hardened. The outer layers of a shrubby and woody stem are impervious to the passage of gases, except for occasional perforations, known as lenticels (page 251), which facilitate respiration. Flowering plants are roughly classified into herbs, shrubs and trees. Herbs die off at the end of each flowering season, whilst the woody framework of shrubs and trees persists to bear new flowers and leaves annually, as well as to increase in dimensions. Shrubs and trees are normally distinguished in that the former branch right down to the ground level, whereas the lower part of the trunk of a tree bears no branches. Aerial shoots become modified, fulfilling various

purposes, most important amongst which are protection, climbing and propagation.

Protective Shoots

Protection against animals is effected by the production of thorns, or **spines**. In the hawthorn, for example, the thorns are modified shoots,

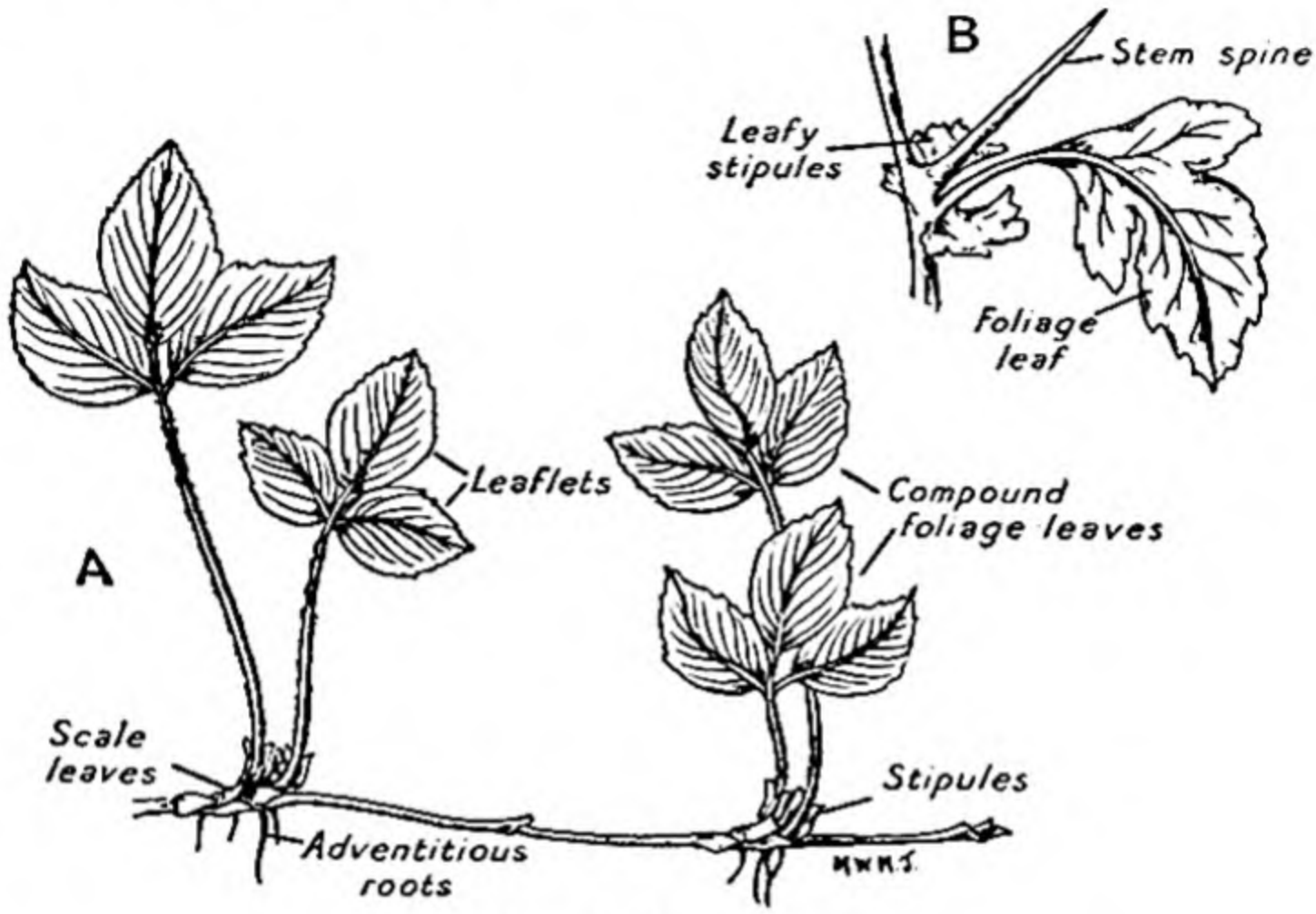


FIG. 162 – Modified aerial stems.
A., Runner of the Strawberry; *B.*, Spine of the Hawthorn.

whereas the branch stems of Butcher's broom become flattened and pointed. In this plant the leaves are reduced to vestiges, the expanded stems facilitating photosynthesis (Chapter 23). Such stems are known as **cladodes**.

Climbing Shoots

Some shoots are modified to form **tendrils**. In many cases these are derived from leaves, as in the sweet pea, for example. But in others they are modified stems. Instances of this are afforded by the vine and the Virginia creeper. Each tendril arises opposite a leaf, this being explicable on the grounds that the branching is sympodial (page 242), the main axis being continued as the stem arising in the axil between the tendril and the leaf, after which the tendril bends away.

Propagatory Shoots

Shoots are modified in various ways, and facilitate propagation. Though varied in structure these propagatory shoots, whether above or below ground, have one important feature in common. Each is essentially

a stem, bearing at least one bud. In the case of a tree the buds (see page 256) remain dormant in the winter and in this condition survive until they can produce new leafy shoots. The same is fundamentally true of all structures designed to facilitate vegetative propagation – *i.e.* reproduction or perpetuation without the production of seeds. The formation of such buds is generally associated with the laying down of food reserves, so that at the suitable season the buds may continue their suspended growth. These common features should be continuously borne in mind as the following description of propagatory shoots is read. A **runner** is an axillary stem growing horizontally along the surface of the ground and taking root at the nodes. An example is afforded by the strawberry. A **sucker** is similar to a runner except that a sucker arises below the level of the ground, comes to the surface and then runs along the surface of the soil. Mint is propagated by suckers. A **stolon** is a branch which, arising above the ground, takes root wherever it makes contact with the soil. All the above are known as **creeping stems**.

Subterranean Shoots

Subterranean shoots are formed in adaptation to vegetative propagation – *i.e.*, reproduction or perpetuation without the formation of seeds. They all have in common the property of acting as storage organs, surviving periods unfavourable to growth in a dormant condition within the soil. According to their various structures they are subdivided into four types.

A **bulb** is essentially a subterranean bud, the stem of which is very

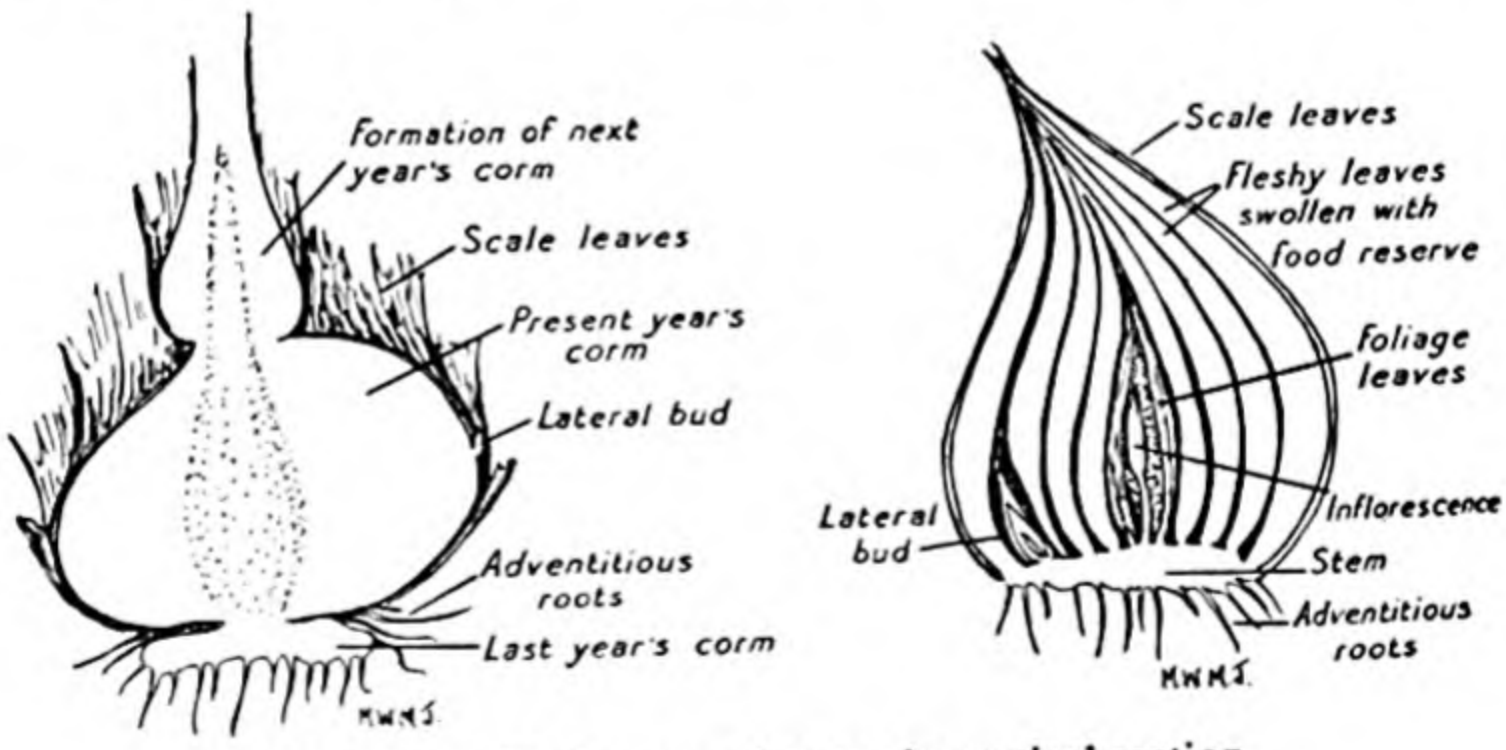
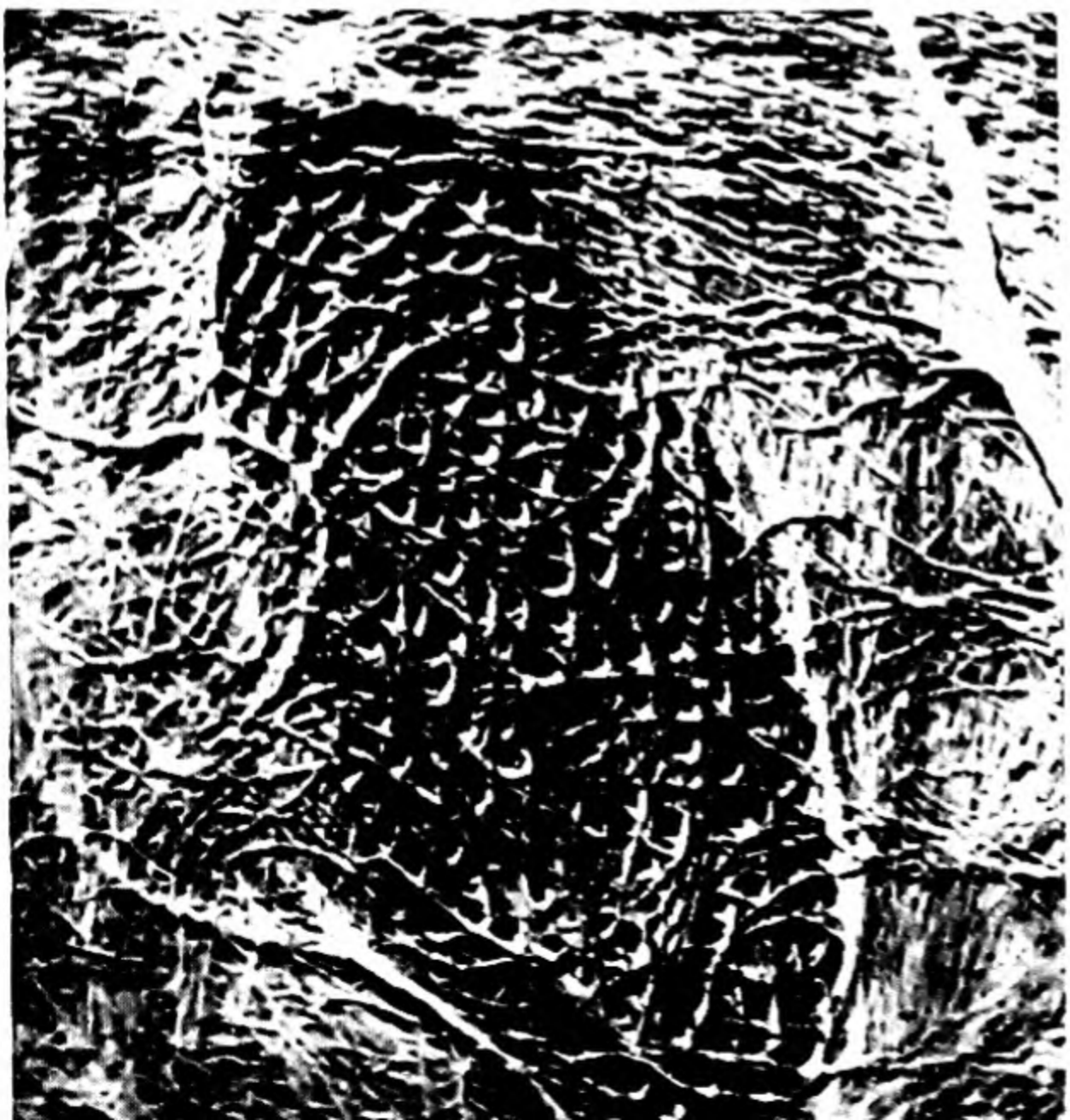


FIG. 163 – Underground stems in vertical section.
Left, A corm; *Right*, A bulb.

much reduced, whilst the leaves have become thick and fleshy, containing large reserves of food. If the scale leaves, usually thin and membranous in this case, enclose the whole bud the latter is described as **tunicated**, whilst if the scale leaves are short and overlap considerably the bulb is

Above Ultrafine section of a chloroplast of *Aspidistra* (By courtesy of Prof A Frey-Wyssling From *Endeavour*, No 53 1 C 1)



Left Pit membrane of a simple p in the radicle of maize (By courtes of Prof A Frey-Wyssling Fro *Endeavour*, No 53 1 C 1)

Above: Ultraviolet photomicrographs of heads of living mammalian spermatozoa, showing strong absorption of radiation by the nucleic acid in the nucleus. (X 4,000 approx.) *Left*, Bull; *Right*, Golden Hamster. (By courtesy of Dr M. W. H. Bishop, Dr C. R. Austin and Mr M. H. Young. From *Endeavour*, No 63. I.C.I.)

Right: Scyphistoma of *Aurelia aurita*, hanging down from a rock. (By courtesy of Dr Douglas

described as **scaly**. The onion is an example of a tunicated and the lily of a scaly bulb. New bulbs arise in the axils of the scale leaves of the old, and are often placed at a convenient depth in the soil and distance from the parent bulb by the development of contractile roots.

A **corm** differs from a bulb in that the bulk of its substance is swollen stem, invested in only a thin covering of scale leaves. As with the bulb new corms are formed in the axils of the upper scale leaves. *Gladiolus* and *Crocus* are propagated by means of corms.

A **tuber** is a swollen, subterranean shoot, occurring normally at the end of a single stem as a result of localised storage. The scale leaves are very much reduced, whilst the buds arise in their axils. The potato is a good

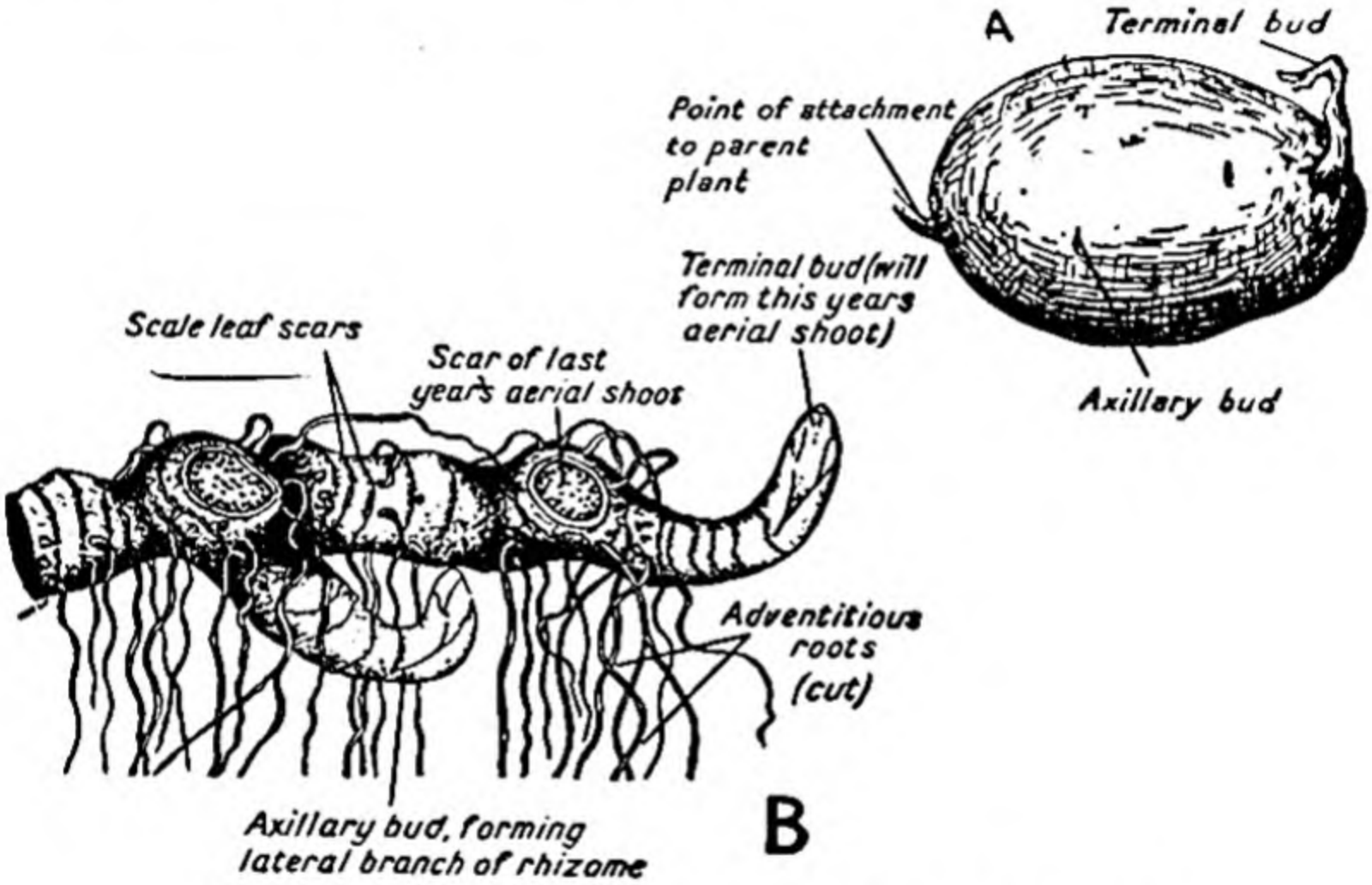


FIG. 164 – Underground stems. *A.*, Tuber; *B.*, Rhizome.

example of a tuber, the 'eyes' being in fact the buds. The buds give rise to aerial shoots, whilst new tubers are formed annually from new subterranean shoots. So-called 'seed' potatoes are, of course, merely tubers.

A **rhizome** differs from the above types in that it continues to grow horizontally from year to year a short distance below the level of the ground. It usually bears scale leaves, whilst scars at intervals indicate the position of scale leaves of previous years. The new plants are produced as a result of the formation of lateral buds. At each growing season one branch forms the new aerial shoot, whilst the other continues its subterranean growth. Examples are afforded by *Iris*, Solomon's seal and bracken.

In all these subterranean shoots a considerable quantity of food material is passed downwards from the flowering shoot at the end

of the growing season, becoming localised in the subterranean storage organ.

Branching

The angle between a leaf and the stem from which it arises is known as an **axil,** and in these axils branches are derived from buds. The behaviour of the main axis and the lateral branches affords a criterion for the classification of types of branching. If the main axis continues its growth so that it is always at a higher level than any of the lateral branches the branching is said to be **racemose** and the structure formed a **monopodium.** If, on the other hand, the main axis grows but little after a lateral branch has arisen, the branching is described as **cymose** and the structure as a **sympodium.** The zig-zag form of this sympodium often becomes so straightened that the whole appears at first glance like a main, central axis. Conifers afford excellent examples of monopodial branching, whilst sympodial branching is apparent in the elm and lime. A modification of the simple type of sympodial branching is seen, for example, in the lilac and mistletoe, where two lateral branches, instead of the usual one, are formed to replace the main axis. In some trees – e.g., *Pinus* – the majority of the lateral branches remain short and are known as **dwarf shoots,** appearing as collections of leaves.

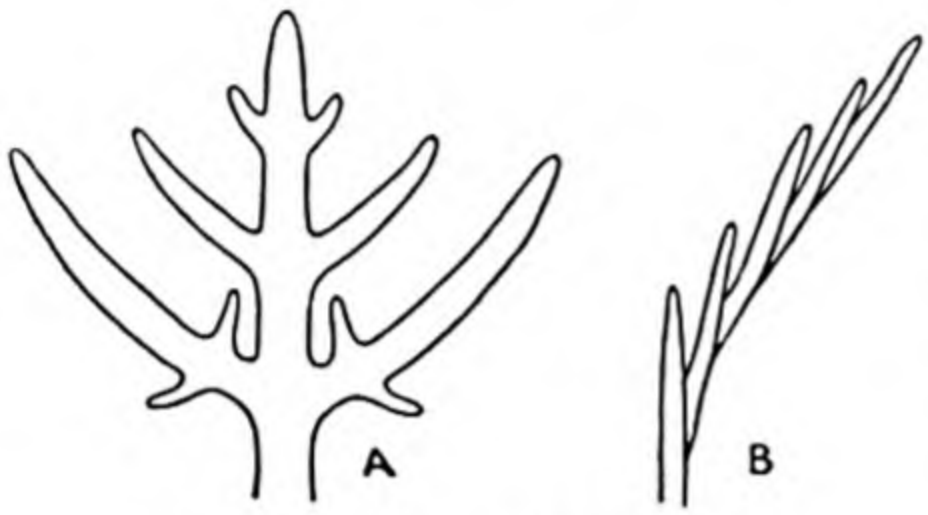


FIG. 165 – Types of branching.
A., Monopodial (Racemose); *B.*, Sympodial (Cymose).

Internal Structure

So far only the broad, external features of the structure of the shoot have been considered. This constitutes **morphology.** It is now necessary to investigate the structure and disposition of the tissues comprising the stem. The stem is composed of various types of cell, characteristically arranged. The arrangement differs somewhat according to habitat, but here a typical mesophyte (page 258) will be described. The structure of the the stem of an aquatic plant is outlined on page 651. The structure of the individual cells is described in Chapter 20. At present it is their distribution, to form various structures and layers, which must be studied. Before this can be attempted it is necessary to note the division of Angiospermae into two groups, known respectively as **Monocotyledons** and **Dicotyledons.** These are named primarily according to the number of cotyledons (Chapters 15 and 31) formed in the embryo plant, though

certain other characteristic differences exist, amongst them being the internal structure of the stem. The dicotyledonous stem will be considered first.

Young Stem

This is best studied in transverse section, as shown in Fig. 166. Enclosing the stem is a single layer of cells, constituting the **epidermis**. Their outer walls are cuticularised (page 305), whilst chloroplasts are normally absent or scarce. Minute pores may also be found in a young stem. Each is a **stoma**, and its margin is formed by a pair of guard-cells. Stomata are, however, more characteristic possessions of leaves, and a detailed description of their structure will be reserved for Chapter 15. Within the epidermis is a many-celled layer, known as the **cortex**. The cells are of fairly regular shape, though air-spaces may be included between them. The walls usually remain thin, though they may be thickened at the corners to form collenchyma (page 321). The cortex is bounded on its inner side by the **endodermis**. This is a single layer of cells, and is usually rich in starch-content. Its walls are frequently thickened, especially laterally. Immediately within the endodermis a layer of fibrous cells,

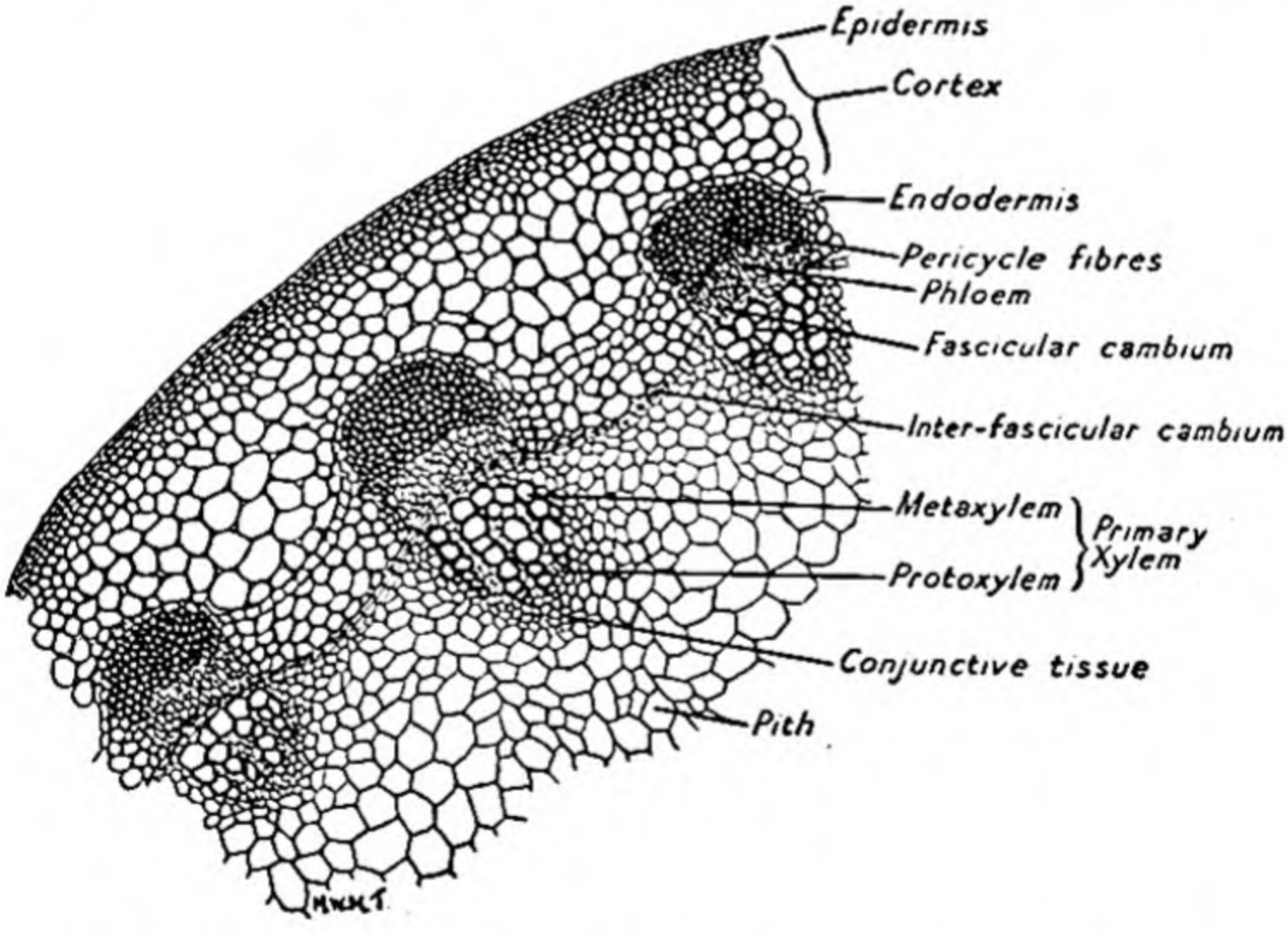


FIG. 166 – Transverse section of part of the young stem of a Sunflower (*Helianthus*).

constituting the **pericycle**, occurs. This layer, together with the remaining central tissue, constitutes the **stele**. The pericycle is usually several cells thick. The most important contents of the stele are the **vascular bundles.**

These are arranged in a broken ring, embedded in ordinary, thin-walled cells, forming the **pith**. The structure of the individual vascular bundles is very important.

Vascular Bundles

Each vascular bundle is normally differentiated into three layers, lying on a common radius. On the outer side is a group of cells constituting the **phloem**, whilst towards the centre of the stem is the thick-walled **xylem**. The two are connected by a strand, several cells thick, forming the **cambium**. This condition will be made clear by reference to Fig. 166. The types of cell which go to constitute the phloem and xylem are described in Chapter 20. It is sufficient here to note that the function of the cambium is to form xylem and phloem. Such a tissue, ultimately giving rise to cells unlike its own, is described as **meristematic**. This is more fully discussed on page 245. Consequent upon their mode of formation the oldest parts of the xylem and phloem are those situated farthest away from the cambium. They are known respectively as the **protoxylem** and **protophloem**, formed actually from procambial strands (page 248). The vessels (page 337) of the protoxylem are smaller than those of the younger xylem, known as the **metaxylem**. Interspersed amongst the cells of the xylem and phloem is ordinary parenchyma, whilst the whole bundle is often invested in a covering of such cells, forming the **medullary sheath**. This simple type of arrangement of the vascular elements may be seen, for example, in the young stem of *Helianthus*. With the xylem and phloem lying on the same radius the

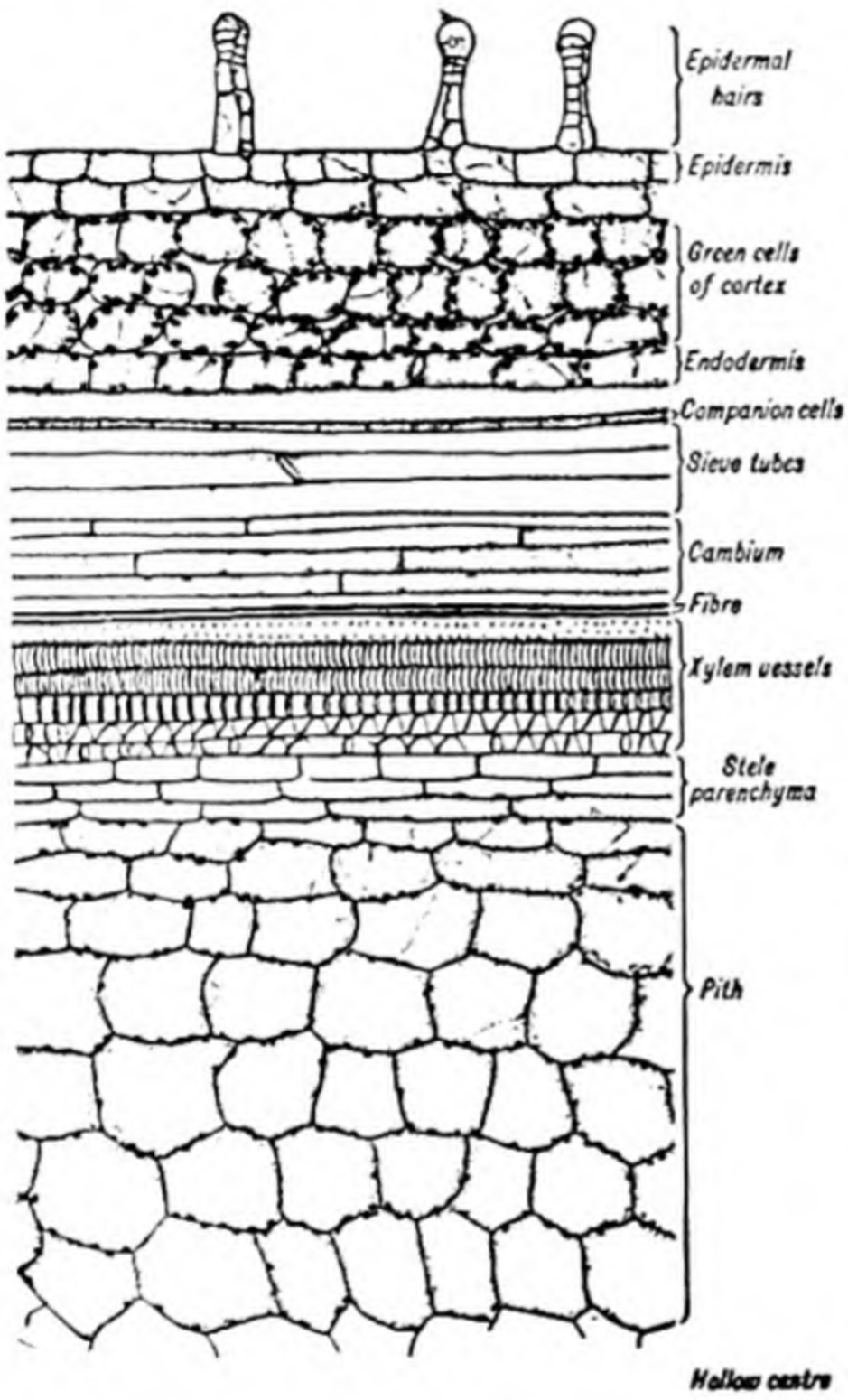


FIG. 167 – Longitudinal section of a Marigold stem.
Successively from the outside appear hairs, epidermis, cortex, endodermis, phloem cambium, fibres, xylem, stele parenchyma and pith.

bundles are described as **collateral.**

In the vegetable marrow (*Cucurbita*) the bundles are arranged in the form of a double ring, those of the inner ring being larger than, and alternating with, those of the outer. The individual bundles differ from those described above in that there is an additional layer of phloem within the protoxylem, from which it is separated either by parenchymatous cells or by another cambial layer. Such an arrangement is described as **bicollateral.**

Elongation of Stem

The only part of the stem, other than the cambium, where active cell-division is proceeding is the tip. Since all the various tissues of the stem

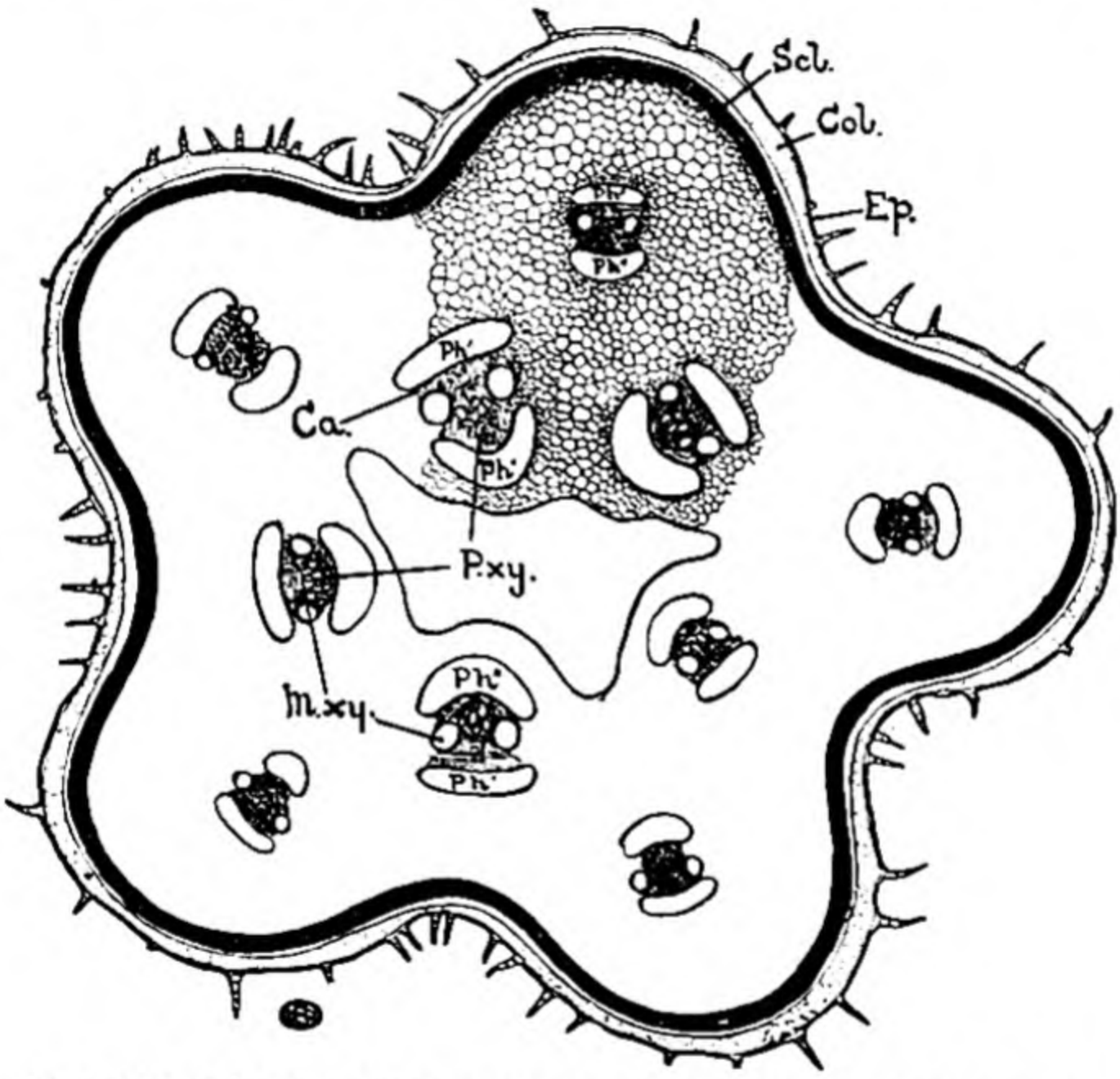


FIG. 168 – Diagram of a transverse section of a stem of the Vegetable Marrow (*Cucurbita*). (From 'Plant Form and Function', by F. E. Fritsch and E. J. Salisbury. Bell.)
Ca., cambium; *Col.*, collenchyma; *Ep.*, epidermis; *M.xy.*, meta-xylem; *Ph'.*, outer phloem; Ph''., inner phloem; *P.xy.*, protoxylem; *Scl.*, sclerenchyma (black).

are derived from the products of this division the tissues constituting the tip must be described as meristematic. As already pointed out (page 244) the cells of a meristem are characterised by their powers of division. By this process they not only have to maintain the existence of the meristem

itself, but also give rise ultimately to the permanent tissues of the plant through differentiation of some of their products. At the apex of any growing shoot is a bud, consisting of a central, dome-shaped mass of cells, enclosed within a series of leaf rudiments, or **primordia**. The apical meristem and young leaf primordia are covered by a thin cuticle, continuous with that of the mature shoot. The cells of this region are small

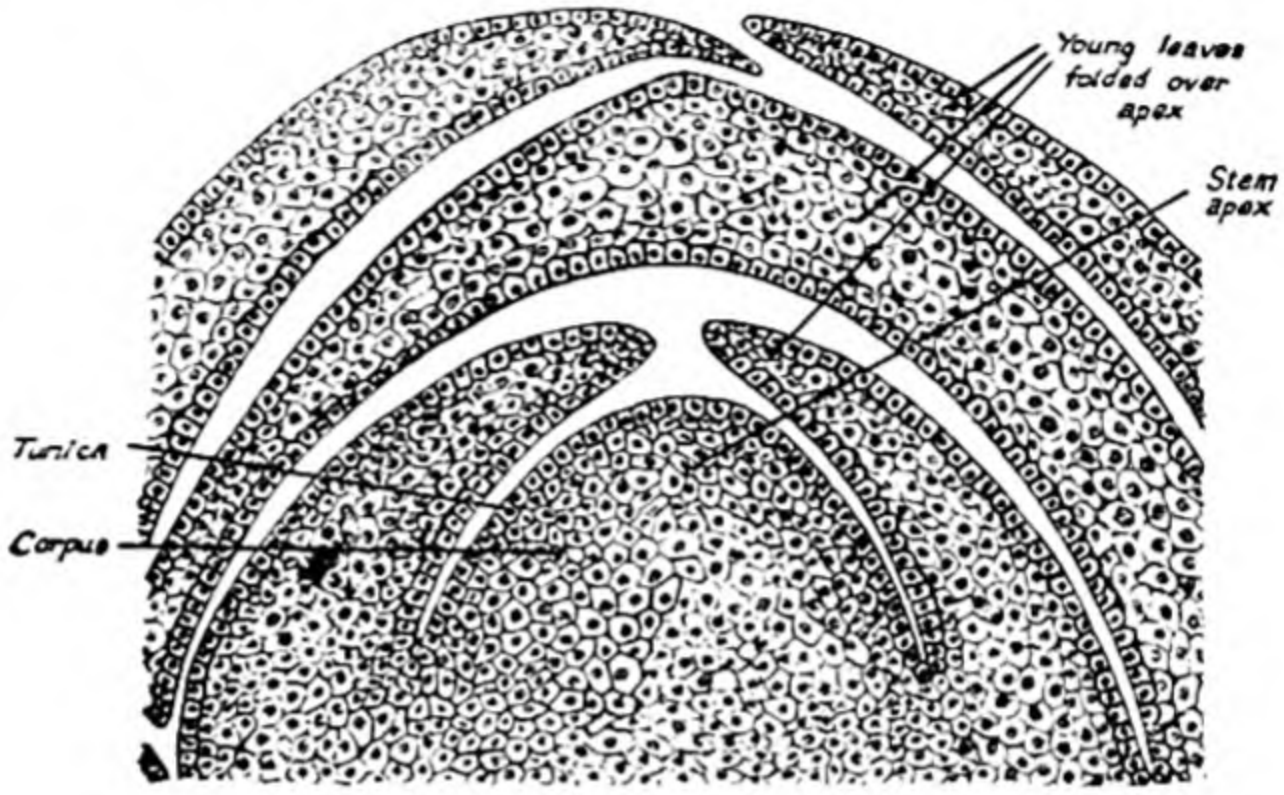


FIG. 169 – Longitudinal median section of a stem apex (Lilac).

and thin walled, possessing spherical nuclei. Protein synthesis occurs rapidly within them and there are no inter-cellular spaces. The apical meristem itself is stratified. As long ago as 1868 Hanstein described three zones, or *histogens*. These were a central *plerome*, surrounded by a *periblem* several cells thick, and the whole covered by a single-celled layer, the *dermatogen*. Although this concept is of some value descriptively, putting emphasis on the specific destinies of the various layers, it does not provide a true developmental picture, for by the time these layers are distinguishable the truly meristematic region of the stem apex has practically been left behind. The modern interpretation is that two regions may be recognised at the stem apex, each characterised by the mode of division of its component cells. The outer layer is the **tunica** and its cells divide anticlinally – i.e., new walls are laid down at right angles to the surface. Thus this layer increases in area but not in thickness, which remains constant for any given type of plant at from one to four cells in extent. The tunica encloses the **corpus**, whose cells divide in all possible planes, so that the corpus increases in volume. The corpus itself may be further subdivided into a peripheral *flank meristem* and a *file*, or *rib-meristem*, at the base of the central portion. The cells of the former are small and divide rapidly, giving rise to the foliar buttresses upon which the leaf primordia are constructed, and also to the procambial strands (see below) from which the vascular elements are derived. In the file

(rib-meristem) some differentiation of the cells has already taken place: indeed, some authorities describe this region as a *sub-meristem*. As the cells divide the products become orientated into columns parallel with the axis of the plant. The cells also become vacuolated, due to the increased plasticity of their walls and the accumulation of osmotically active sugars. Thus elongation occurs in this region and internodes arise, separating the nodes where leaf primordia occur.

Some authorities describe, at the extreme apex of some plants, a

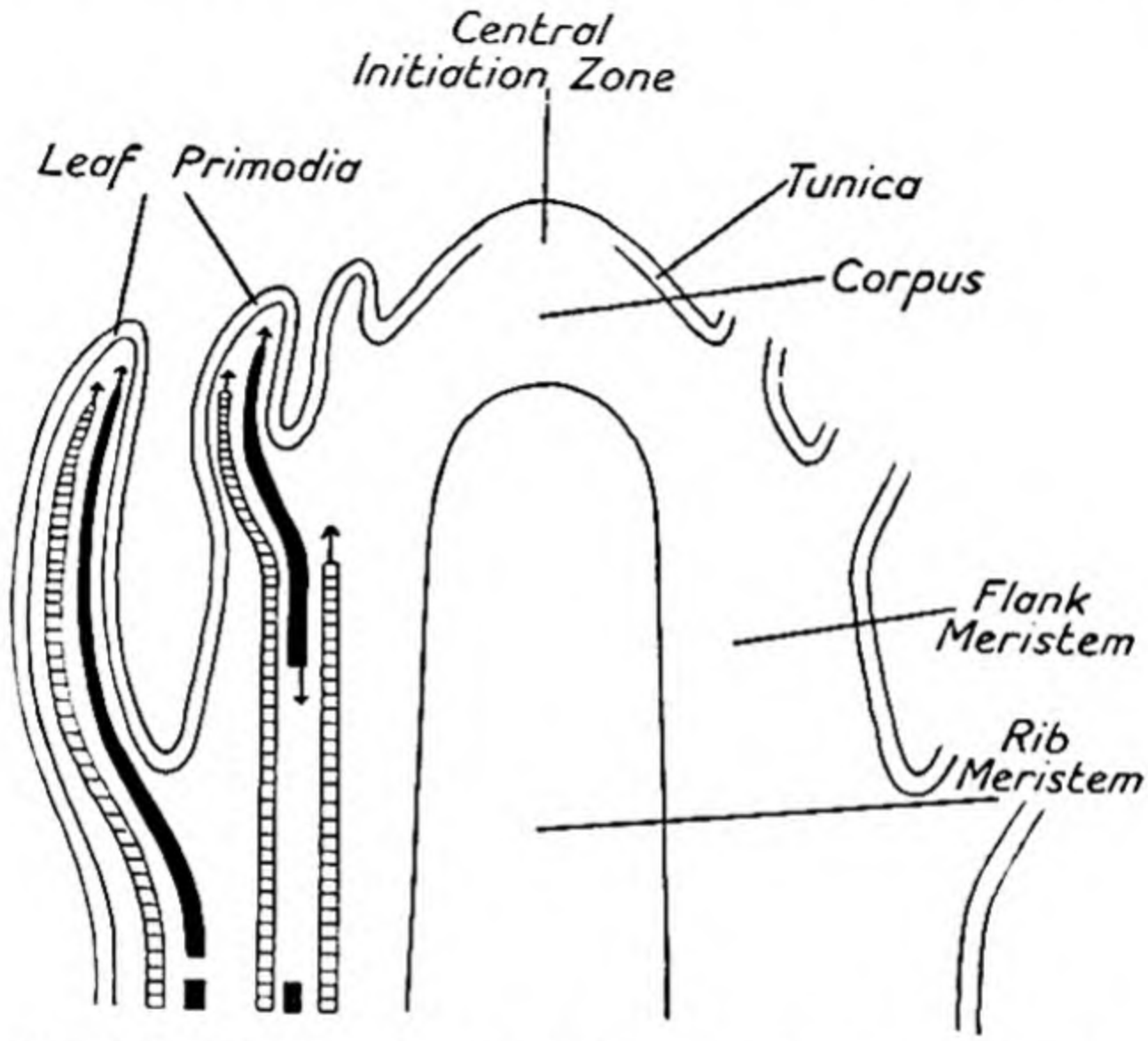


FIG. 170 – Diagram of a vertical section of a typical stem apex, bearing leaf primordia. Xylem is shown in black and phloem is cross-hatched: arrows indicate direction of differentiation.

central initiation zone, the products of division of whose cells give rise to both tunica and corpus.

Before considering events farther back in the stem, where further differentiation occurs, including the formation of the vascular elements, it is necessary to investigate the method of origin of leaf primordia. The tunica increases rapidly in extent and this leads to an orderly folding outwards of this layer when the cross-sectional area of the stem apex reaches a maximum. Immediately below this evagination the cross-sectional area falls to a minimum, only to rise again to a maximum as the point of formation of the next primordium is approached. The time interval between the initiation of successive primordia is termed a **plastochron**. At each evagination of the tunica the cells of the flank

meristem build up a foliar buttress, so completing the leaf primordium.

The eventual differentiation of vascular elements is best considered for stem and leaf simultaneously, since they are closely associated. Extending downwards into the stem, usually from the outer layers of the corpus, is a tubular meristematic ring. Occasionally the whole of this ring may become procambium, but in most cases subsequent differentiation is confined to localised portions of it, termed **procambial** (or *desmogen*) **strands**. At first the cells of these strands divide irregularly, but soon the divisions become predominantly tangential, so that the products are arranged radially. From this point onwards the erstwhile procambium is termed **cambium**.

Every procambial strand arising in the stem is continuous with that developing in a leaf primordium – i.e., it becomes a **leaf trace**. Subsequent differentiation into vascular elements may not commence until three or four plastochrons later. Phloem appears first, sieve tubes becoming differentiated progressively from the lowest point in the stem strand, where linear continuity with established phloem tissues exists, upwards towards the apex of the leaf. Xylem formation from the inner face of the strand occurs first near the base of the primordium and soon extends upwards into the developing leaf. Somewhat later, short tracheids are differentiated downwards to close the gap. These may extend for some distance alongside existing xylem before vascular continuity is established.

Axillary buds are formed exclusively from the superficial tissues of the growing point, their origin being consequently described as **exogenous**. Each arises immediately above a leaf primordium and in exactly the same vertical plane. Once initiated, the developmental process in a lateral shoot follows the same lines as that described above. It should be carefully compared with that of branch roots (page 294).

Secondary Thickening

Strictly speaking this commences as soon as the vascular elements proliferated by the cambium assume a radial arrangement. This is particularly obvious where the whole meristematic ring gives rise to xylem and phloem from the outset – i.e., where there are never separate vascular bundles. Where these latter do appear the portions of meristematic ring between them may simply develop more slowly into cambium or, if the cells have become parenchymatous, these parts of the ring may become cambium by a process of de-differentiation from the parenchyma. In any event a complete ring of cambium is ultimately reconstituted, that connecting adjacent bundles (where such exist) being described as **interfascicular**. Once completed the cambial ring usually proliferates xylem and phloem around its whole circumference, but in a few cases the interfascicular cambium gives rise to parenchyma, as in the Vine. These wide bands of parenchyma, separating persistent bundles, are termed **primary medullary rays**. In the more typical cases, where the whole ring of

cambium produces new xylem on its inner side and new phloem on its outer face, these tissues are described as *secondary*, distinguishing them from the xylem and phloem of the originally separate bundles, whose

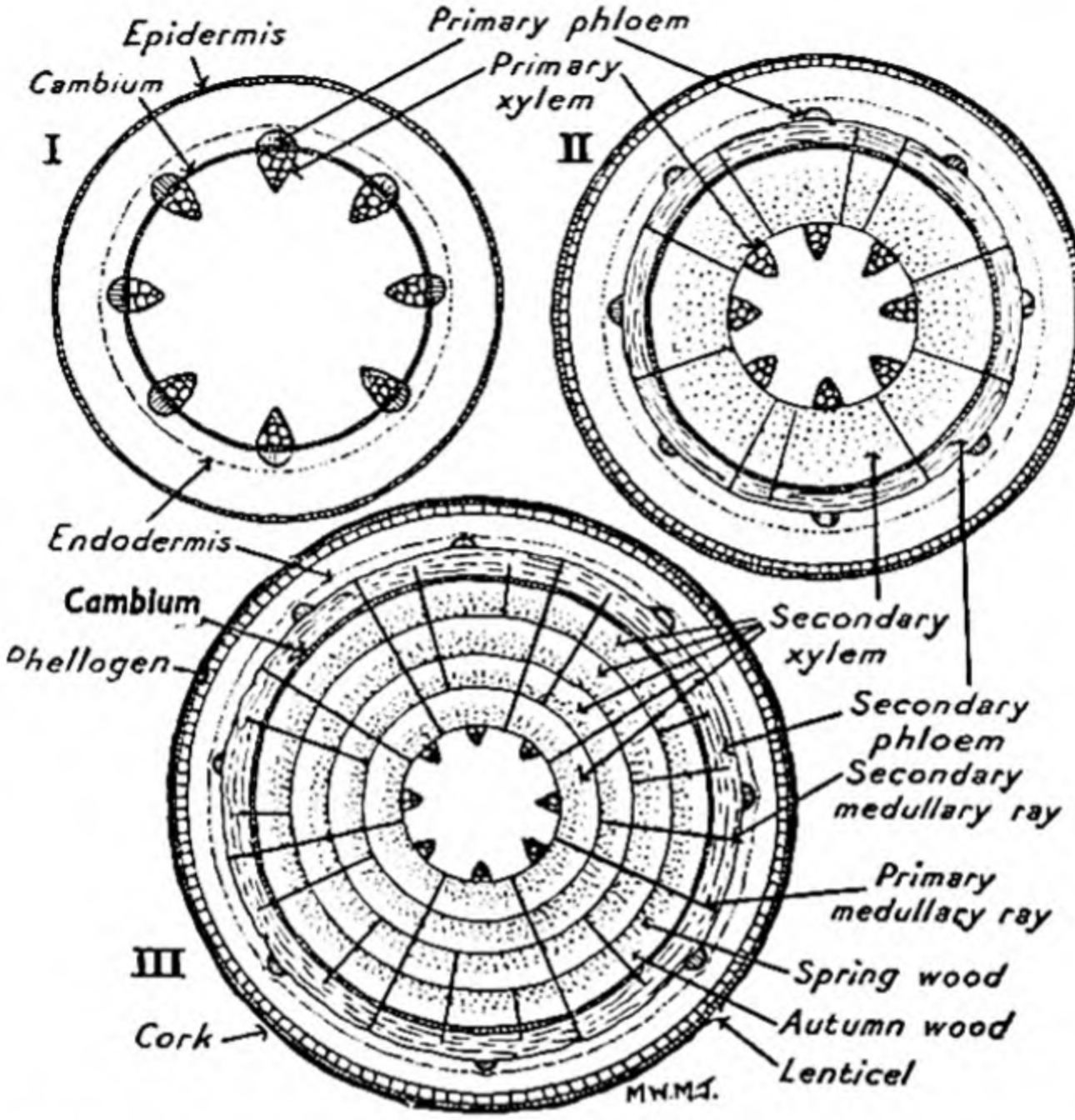


FIG. 171 – Diagrams to illustrate the course of secondary thickening in the stem of a Dicotyledon.

tissues are described as *primary*. Each yearly addition to both layers constitutes an **annual ring**, normally visually apparent in the xylem only. The activity of the cambium, once secondary thickening has commenced, is continuous, except in winter. The secondary xylem formed in spring and summer conveys a great deal of water and dissolved salts from the root to the leaves. Accordingly the vessels which constitute it become distended. But vessels formed in the autumn remain closed, owing to their having no similar function to perform. As a result a thickened stem consists of a number of concentric cylinders of alternating summer and autumn wood, the former being wide and the latter narrow and compact. This is clearly seen on examination of the cut surface of the trunk of a felled tree. Counting up the number of either light or dark rings therefore gives a reasonable estimate of the age of the tree. It may not be

perfectly accurate in an old tree, since compression may have resulted in the fusion of some of the inner layers. Small portions of cambium may, from time to time, give rise to parenchyma instead of the usual

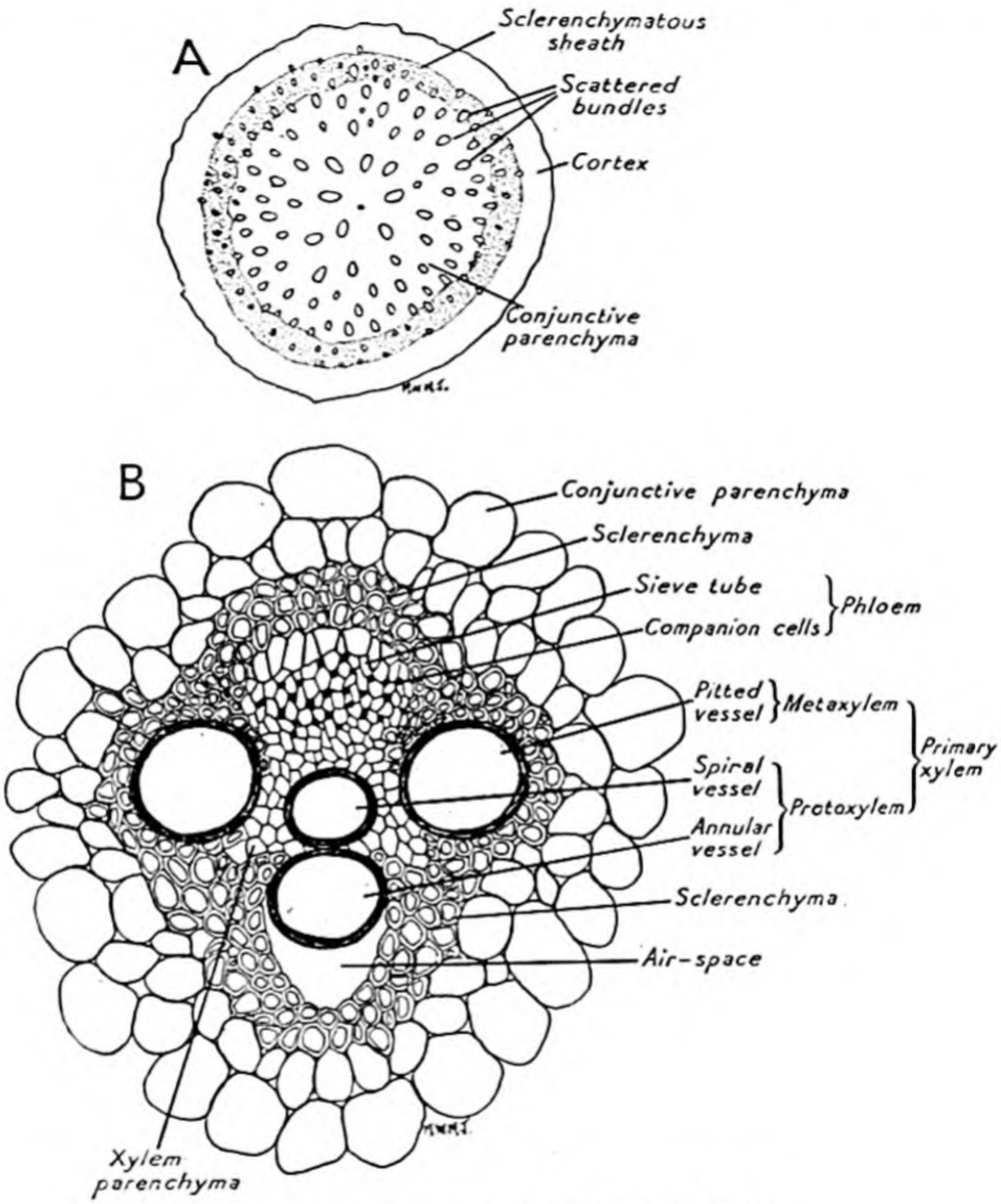


FIG. 172 – The stem of a Monocotyledon.
A., To show the disposition of parts.
B., A single vascular bundle.

xylem and phloem, and in this way **secondary medullary rays** are formed. Being soft celled, the tissues of these rays can be compressed and thus relieve internal pressure. In a felled tree they are apparent as radial cracks in the wood.

Once secondary thickening has commenced a new cambium – the *cork*

cambium, or **phellogen** – arises somewhere between the epidermis and the secondary phloem, its exact position depending upon the actual plant under consideration. The phellogen gives rise to *cork*, or **phellem**, on its outer side, and often to a secondary cortex, or **phelloderm**, on its inner. The walls of the cork cells become impregnated with suberin and are therefore rendered impervious to the passage of water. Thus the cells die. The whole system of layers of cells associated with the phellogen constitutes the *bark*, or **periderm**. At intervals the phellem is interrupted by small aggregates of corky cells, so loosely packed that gaseous exchange is facilitated between the atmosphere and the living cells within. These are the **lenticels.**

Monocotyledonous Stem

Monocotyledonous stems differ from those of Dicotyledons in four respects, namely:

(*a*) There are many more bundles and they are distributed throughout the parenchymatous ground-tissue in no particular configuration. They are more numerous peripherally than in the centre.
(*b*) Cambium is absent from the bundles.
(*c*) The phloem is characteristically without parenchyma.
(*d*) Secondary thickening rarely occurs.

The cortex is not always distinguishable from the stele, whilst each individual bundle is usually enclosed by sclerenchymatous fibres. The cells of the phloem are not interspersed with parenchyma, so that this tissue presents a remarkably regular appearance. The bundles, though of the collateral type, are described as **closed**, since cambium is absent. In those forms where secondary thickening occurs the bundles are still closed. A secondary meristem arises outside the original bundles, proliferating new xylem and phloem, together with fibres and parenchyma in which the new bundles are embedded.

PRACTICAL WORK

Examine, if and when available, the various protective and climbing stems mentioned on page 239. Examine others and decide for yourself whether the modified structures are really stems. (This may perhaps be better left until the first part of Chapter 15 has been studied.) Draw representative specimens.

Examine the various examples of propagatory stems described on page 239. Investigate any others available, deciding into which class they should be placed.

Examine a large number of twigs selected at random and describe their branching. Preface this with a study of a twig from a tree whose form of branching is already known to you. Make representative sketches.

Examine carefully examples of the four types of subterranean shoot.

Draw each. Cut longitudinal sections of a bulb and corm. Draw. In the corm look for the storage region of the previous year. In the bulb notice the incipient formation of a new bulb in the axils of the scale-leaves of the current one. Allow potatoes to 'sprout' by retaining them in darkness. Examine and sketch.

Cut and examine a transverse section of a young stem of *Helianthus* (sunflower) and *Cucurbita* (marrow). Compare their structure with the description and figures in the text. Make first a tissue distribution (or regional) diagram, in which no cells are drawn. Follow this with a high-power drawing of a typical vascular bundle, paying close attention to the size and shape of the component cells and to the relative thickness of their walls. Cut, examine and draw transverse sections of older stems. Prepared specimens of these should also be carefully examined.

Cut, examine and draw a transverse section of a tulip or hyacinth stem as a representative of the Monocotyledons.

Though special stains are employed to distinguish particular tissues a general staining technique for stems may here be practised on really thin sections, enabling the vascular elements to be more readily discerned. If material preserved in 70% alcohol is being used (this is normally best for cutting) the sections are transferred from 70% to 50% alcohol. They are then placed in safranin for not more than fifteen minutes. On removal from the stain they are placed successively in 70%, 90% and two lots of absolute alcohol, allowing about three minutes in each. As a result dehydration is effected. A little clove oil is then added to the second lot of absolute alcohol containing the sections, and the sections are soon transferred to pure clove oil. From this they are placed in light green for up to fifteen seconds. After return to clove oil to remove the superfluous stain they are mounted in Canada balsam. The general ground-tissue will appear green, whilst the vascular xylem and fibres will be clearly differentiated by their red colour.

Temporary stains for the identification of special tissues are given at the end of Chapter 20.

CHAPTER 15

The Leaf

As for the stem, it will be found convenient first to study the gross external structure – i.e., morphology – of the leaf, followed by a consideration of its internal anatomy, as revealed by microscopic examination.

External Structure

A typical foliage leaf is divisible into two parts. It is attached to the stem which bears it by means of a stalk, or **petiole**. This is usually somewhat enlarged at the base, though in some forms the petiole is entirely absent, in which case the leaf is described as sessile. In other cases it becomes expanded to assume the form of a blade – e.g., some species of *Acacia*. Such a structure is termed a **phyllode**. The distal portion of a leaf

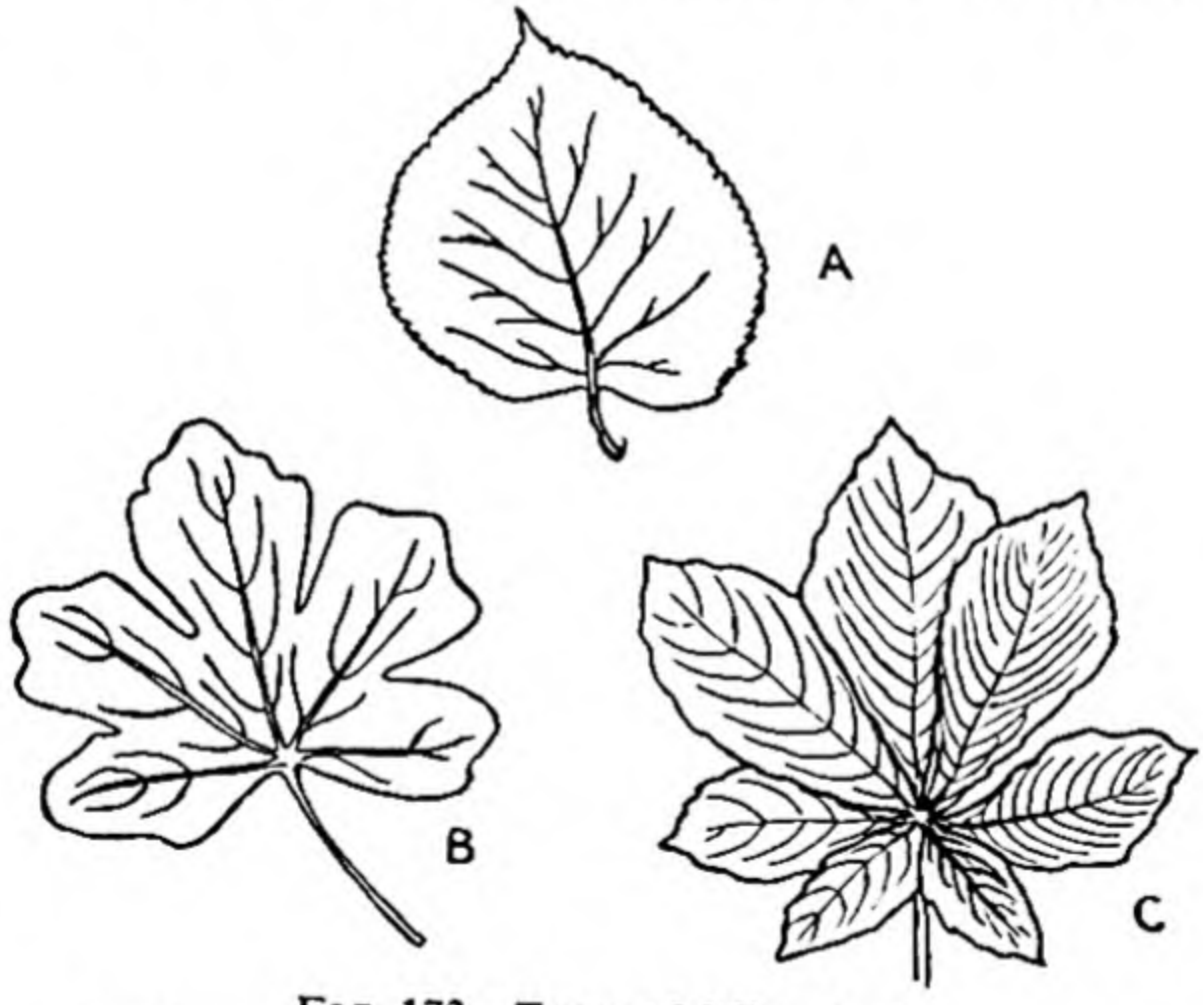


FIG. 173 – Types of foliage leaf.
A., Simple (Lime); *B.*, Divided (Maple); *C.*, Compound (Horse Chestnut).

consists typically of an expanded blade, known as the **lamina**. This is of importance in relation to photosynthesis. The lamina may possess a smooth, regular outline, in which case the leaf is described as **simple**, or it may be subdivided by grooves into large or small lobes, surrounding

an undivided portion in the centre, being then known as **lobed**. Alternatively the leaf may become completely subdivided into lobes, or leaflets, the leaf being then described as **compound**. There are two varieties of compound leaf. In the **palmate** type all the leaflets arise at the same point, whilst **pinnate** leaves are characterised by the regular succession of leaflets, or pinnae, on either side throughout the length of the leaf. A compound leaf may be distinguished from a stem bearing a number of leaves by the absence of axillary and terminal buds.

Arrangement of Leaves

The arrangement of leaves on the stem of a plant is a constant characteristic. Most commonly there is a single leaf at each node, the arrangement being then described as **alternate**. But in others a pair of leaves arise at each node, a condition described as **opposite**. The lilac affords an example. In this type each pair of leaves is usually at right angles to the preceding one. In such a case the arrangement is known as **decussate**. Occasionally the bases of two opposite leaves meet completely to envelop the stem at the node: this condition is known as **connate**, and is exemplified by the teasel. Finally it is possible for more than two leaves to arise at a node, when the arrangement is termed **whorled**. Alternate leaves are typically arranged in a spiral fashion around the stem. In the simplest case passage from the base of one leaf to that of the next involves passing half-way round the circumference of the stem. In this case the relative positions are expressed by saying that there is a **phyllotaxis** (leaf-arrangement) of $\frac{1}{2}$, which obviously results in the leaves occurring in rows on opposite sides of the stem. If in passing completely around the circumference of the stem via the bases of the leaves three leaf-bases are passed through there is a phyllotaxis of $\frac{1}{3}$. The simplest way of determining phyllotaxis is to select a leaf and then find the one next vertically above it. Draw a line from the base of one of these leaves to the other, passing spirally round the stem through the bases of all the intervening leaves. Count the number of leaf-bases passed and the number of complete circuits made of the stem. The former gives the denominator of the fraction expressing the phyllotaxis and the latter the numerator. It will be frequently observed that phyllotaxis varies in different parts of the plant.

Venation

Conspicuous on the surface of most leaves are the veins, actually extensions of the vascular bundles of the stem. In Monocotyledons they run almost parallel to each other and to the longitudinal axis of the leaf. The venation is described as **parallel**. The veins of Dicotyledons branch to form a network, so that this venation is said to be **reticulate**. Of this there are two kinds. In the one – pinnate – there is a main, central vein, whilst in the palmate type there are several veins of equal prominence.

Modification of Foliage Leaves

The average foliage leaf, whose function it is to accommodate photosynthesis, assumes the structure outlined above, but in other cases they become variously modified.

(A) CLIMBING. Many leaves of climbing plants are modified to form **tendrils**. This alteration in structure normally affects only the upper part of the leaf – e.g. sweet pea, where only some of the leaflets are involved,

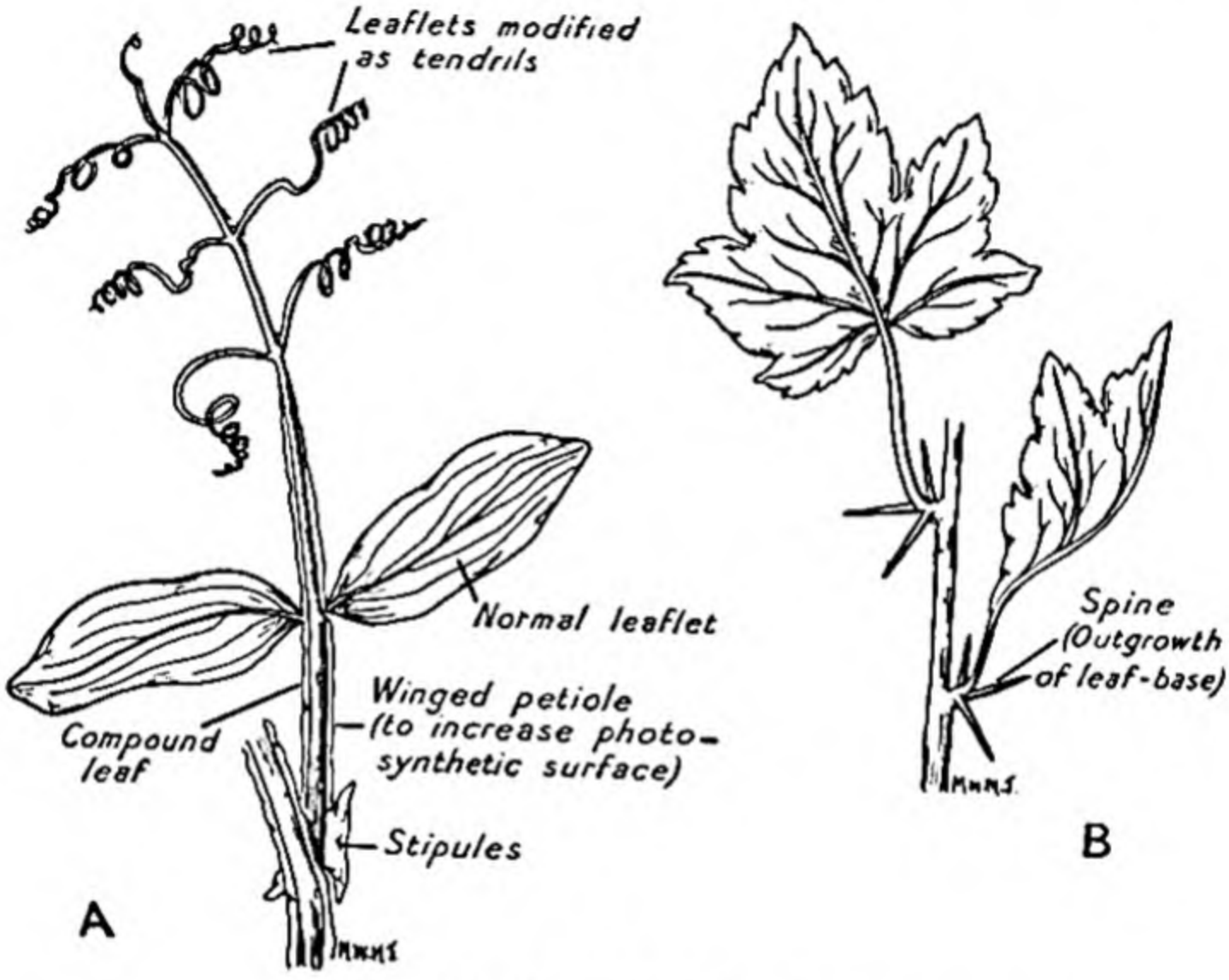


FIG. 174 – Modified foliage leaves.
A., Tendrils (Sweet Pea); *B.*, Spine (Gooseberry).

whilst the loss of surface is compensated by the expansion of stipules (see below), commonly found growing out from the bases of the leaves of this plant, whilst the petioles too may become expanded.

(B) PROTECTION. Wherever the leaf-base is expanded to form a sheath, protection is afforded to axillary buds. In many plants the performance of this function is enhanced by the formation of outgrowths, known as **stipules**, from the leaf-bases, as in the rose and cherry, for example. Leaves bearing stipules are described as stipulate. The relation of stipules to tendrils was mentioned in the preceding paragraph. Further protection may be provided, this time to the plant as a whole, by the formation of thorns, or **spines**. The barberry and gooseberry are examples of plants bearing spines which are morphologically leaves, though in the latter the spine arises from the leaf-base, so that the leaves are themselves

present. That this is so may be detected from the origin of branches from their axils. Thorns may also arise by the modification of stipules, as in the false acacia (*Robinia*). In the gorse both leaves and stems may become modified to form spines.

(C) CAPTURE OF FOOD. In some insectivorous plants the leaves are often modified to form an apparatus for the entrapping of insects. One type, found in the pitcher plants, assumes the form of a depression, guarded by a valve-like structure. Once the insect passes into the bladder thus formed, no escape is possible. Certain cells lining the cavity secrete juices which digest the body-substance of the insect. (See also page 659.)

(D) STORAGE. Some leaves fulfil an important function in respect of storage of various materials. Thus starch grains are deposited temporarily within the leaves of almost all green plants as a result of active photosynthesis (Chapter 23). Bulbs have already been described (page 240), the storage of food being effected by the fleshy leaves. In some xerophytic plants water is stored in the leaves, which become succulent. Houseleeks afford an instance of such plants.

Buds

Buds may occur either at the tip of a stem, when the internodes have not yet elongated, or in the axil between a leaf and the stem which bears it. The former type is described as **terminal** and the latter as **axillary**. It frequently happens that the axillary buds remain dormant, though they may be stimulated to activity by the removal of the terminal bud. Hence the frequent trimming of a hedge, for example, results in the development of the axillary buds, since the terminal ones are cut off, so that the hedge thickens. At times the buds remain dormant for considerable periods – e.g. throughout the winter. This necessitates their protection, which is usually effected by the enclosure of the delicate foliage leaves within a covering of thick scale leaves. The horse chestnut affords a good example of this. Within the scale leaves is a dense mass of hair-like structures, affording further protection. Buds not covered by scale leaves are described as naked. The internal arrangement of the leaves of the bud of the ash is shown in Fig. 175B. When the bud opens, the scale leaves are eventually shed. This results in the formation of a circular scar, and the one immediately below it represents the bud scars of the previous winter, so that the twig in between is one year's growth. A twig commonly shows other scars, roughly triangular in shape. These mark the positions formerly occupied by foliage leaves. Their formation is described more fully when leaf-fall is considered (page 261).

One peculiar form of bud may be noticed. It arises in the axil of a leaf in a position normally occupied by flower buds. Owing to certain resemblances to bulbs (page 240) they are known as **bulbils**, and are common, for example, in lilies.

Reference has already been made (page 240) to vegetative propa-

gation. Here we must notice two methods of artificial propagation practised by man, especially in connexion with fruit trees and roses. In **budding**, a shield-shaped portion of the plant to be propagated is cut out.

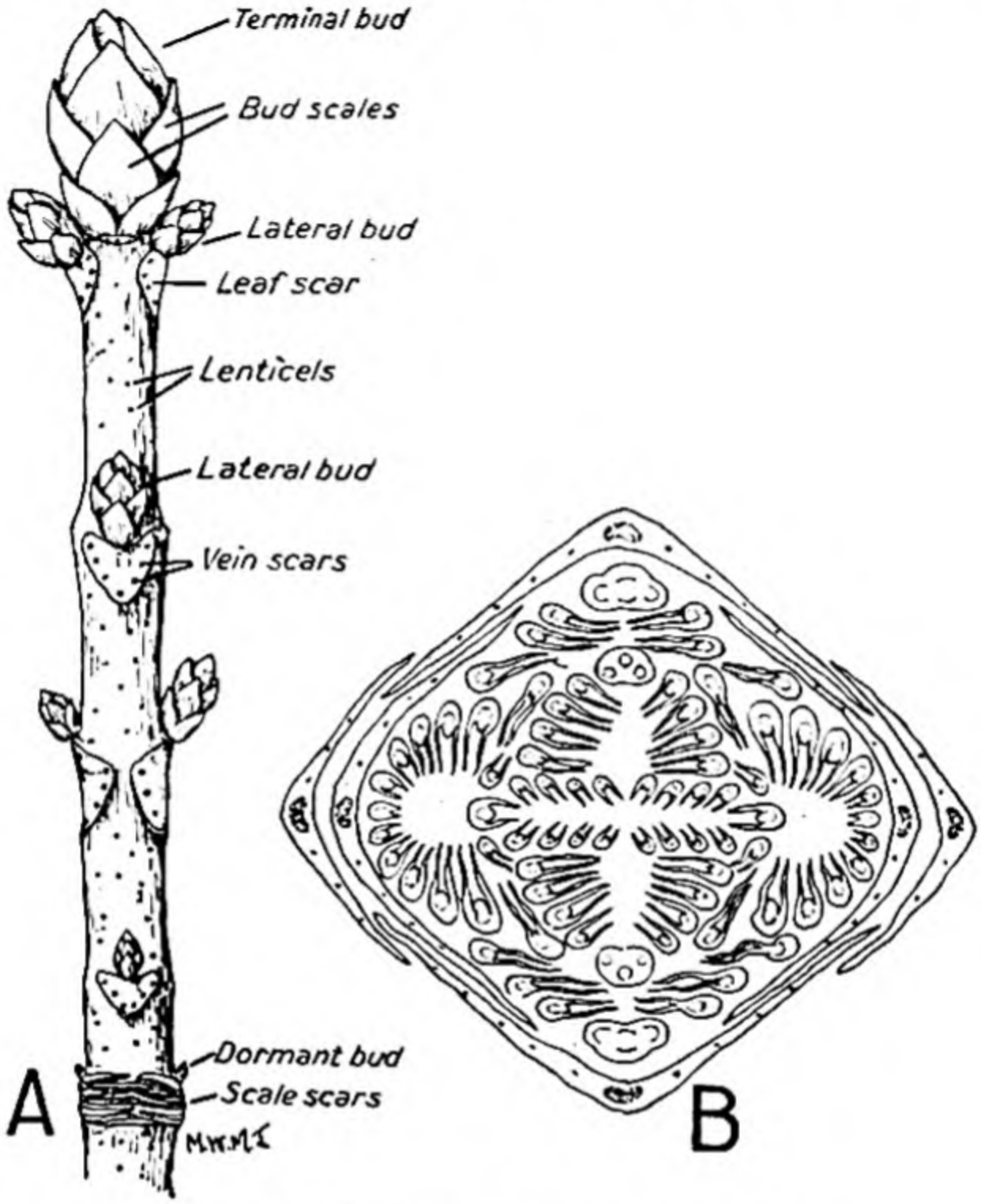


FIG. 175 – The structure of foliage buds.
A., An entire twig of the Horse Chestnut.
B., Transverse section of the bud of the Ash.

This piece must include the bark and all the tissues down to the wood, as well as which it must, of course, bear a bud. It is then introduced into a T-shaped incision in the bark of the stock tree, and the wound is covered with wax, thus affording protection against infection or the drying of the tissues.

In **grafting**, a twig is removed from the plant to be grafted and its tapered end introduced into a slit in the wood of the stock. Here, again, the wound is covered with grafting wax.

In general, budding and grafting can be carried out only between closely related plants, and afford means of propagating any valuable variety of rose or fruit tree on the stem- and root-systems of a wild or

common variety. It is, of course, largely a matter of preserving the genetic constitution (see page 578) of the plant selected for propagation.

The taking of **cuttings** – e.g. twig of privet – is a well-known method of artificial propagation. A twig bearing a bud is torn off and planted. Roots, described as adventitious (page 289), arise from the base of the stem and the bud continues its growth, so that a new plant is formed.

Types of Leaf

It must be borne in mind that a variety of structures in a flowering plant, besides those comprising the ordinary foliage, are known as leaves. Each will be mentioned now, though detailed consideration of some of them will be retained for later chapters.

(A) COTYLEDONS. The first leaves to appear in the embryo plant are known as cotyledons. According to the number of these structures present, Angiospermae are classified as Monocotyledons (one) and Dicotyledons (two). Their structure and significance are more fully discussed in Chapter 31.

(B) PROPHYLLS. The leaves produced in the seedling immediately after the cotyledons often exhibit simple structure, even though the rest of the foliage leaves may be complicated. These leaves, intermediate in form between cotyledons and foliage and remaining at the base of the stem, are known as **prophylls.**

(C) BRACTS. Flowers are borne on stalks, which arise in the axil between a leaf and stem, such a leaf being frequently characterised by a marked difference from the remainder of the foliage leaves. It is termed a **bract**. Frequently bracts are arranged in clusters, surrounding a collection of flowers. This is well illustrated in the family Compositae (page 631), where the collection of flowers constitutes an inflorescence, and the cluster of bracts surrounding it an **involucre.** In the wild arum a single bract completely encloses the inflorescence: it is known as a **spathe**. Leaves sometimes occur on the actual flower-stalk, and these are termed **bracteoles**. There are frequently two of these in Dicotyledons and one in Monocotyledons.

Internal Structure

Having thus acquired a knowledge of the external form of leaves it is essential now to consider their internal anatomy. For this purpose a typical dicotyledonous leaf will be selected, growing in the presence of average light and moisture. A plant adapted to such conditions is termed a **mesophyte,** in contrast with hydrophytes and xerophytes, living respectively in water or in arid situations. A transverse section, as illustrated in Fig. 176, affords the best means of investigation of internal structure.

Limiting both the upper and the lower surface is a single layer of cells, constituting the **epidermis**. The cells of this layer are for the most part

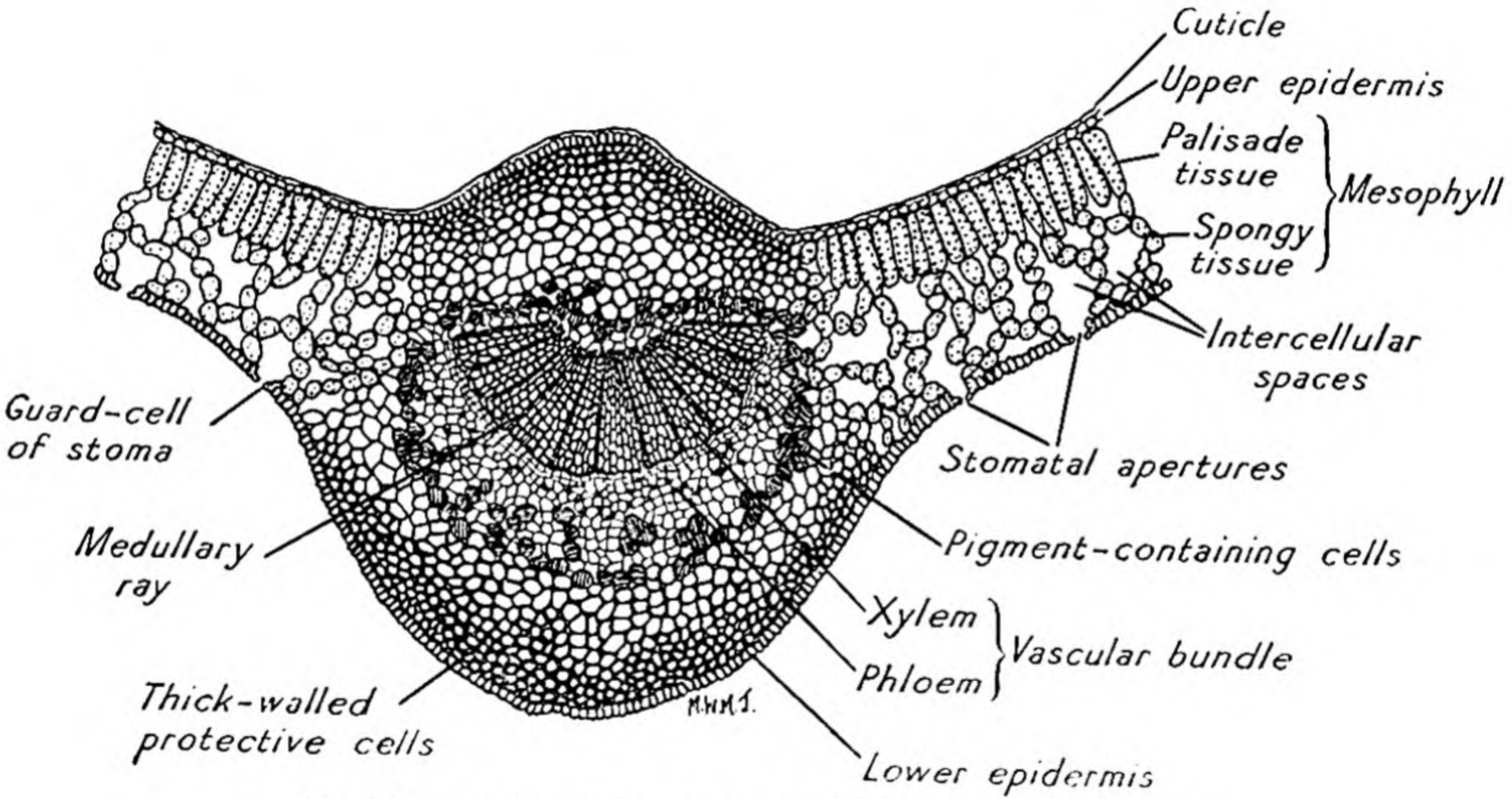


FIG. 176 – Transverse section of a foliage leaf, passing through the mid-rib.

colourless, though the **guard-cells** (see later) contain chloroplasts. On the outer surface of each epidermis is a **cuticle**, perforated at intervals, especially on the lower side, by minute pores, known as **stomata**.

Beneath the upper epidermis is a layer of cells, known as the **palisade layer**. It is normally composed of one or two rows of cells, considerably elongated at right angles to the surface of the leaf and frequently enclosing small air-spaces between them. Lining each cell is a thin layer of cytoplasm, whilst the centre is occupied by a more or less transparent cell-sap. The cytoplasm contains discoid chloroplasts, usually collected along the elongated walls.

The **spongy parenchyma**, situated beneath the palisade layer, is composed of irregularly-lobed cells, making random contact with each other, so that a number of inter-cellular spaces are formed. This is important for the circulation of atmospheric gases through the leaves (and subsequently to other parts of the plant); in addition, the comparatively large surface of the cells of this layer is of extreme importance in the absorption of carbon dioxide prior to photosynthesis (Chapter 23). There are relatively few chloroplasts in the cells of the spongy parenchyma. The palisade layer and the spongy parenchyma are collectively referred to as the **mesophyll**.

Veins

The position occupied in the leaves by the vascular bundles is indicated externally by the veins, the disposition of which is described on page 254. Each bundle is seen in transverse section to consist of xylem and phloem, and in some leaves a cambium is present. The xylem is uppermost, consisting of a few rows of vessels, interspersed with parenchyma. The protoxylem is nearer the upper surface of the leaf. The phloem lies towards the lower epidermis. Each bundle is enveloped in a covering of parenchymatous cells, whilst beneath the phloem there is usually much collenchyma. As a result of repeated branching the bundles in the leaves become progressively reduced, until at length the phloem practically disappears, whilst the xylem consists of tracheids (page 339) with little or no wood parenchyma. The vascular bundles are in continuity with those of the stem through the petiole. It will be evident, therefore, that the xylem must appear towards the upper surface of the leaf, since it is towards the centre in the stem. A bundle from a leaf may pass for some distance down the stem as a separate unit, but in most cases all the leaf bundles eventually coalesce to form a comparatively small number of bundles in the stem.

Stomata

Mention has already been made of minute pores occurring in the upper, and to a greater extent in the lower, epidermis. The structure of a single stoma must now be considered in more detail. Each is completely

surrounded by a pair of **guard-cells** (Fig. 251, page 404). Seen from above these are sausage-shaped structures, in contact at the two ends and with their concavities directed inwards. Thus a pore is enclosed. The guard-cells are smaller than those of the remainder of the epidermis, whilst their

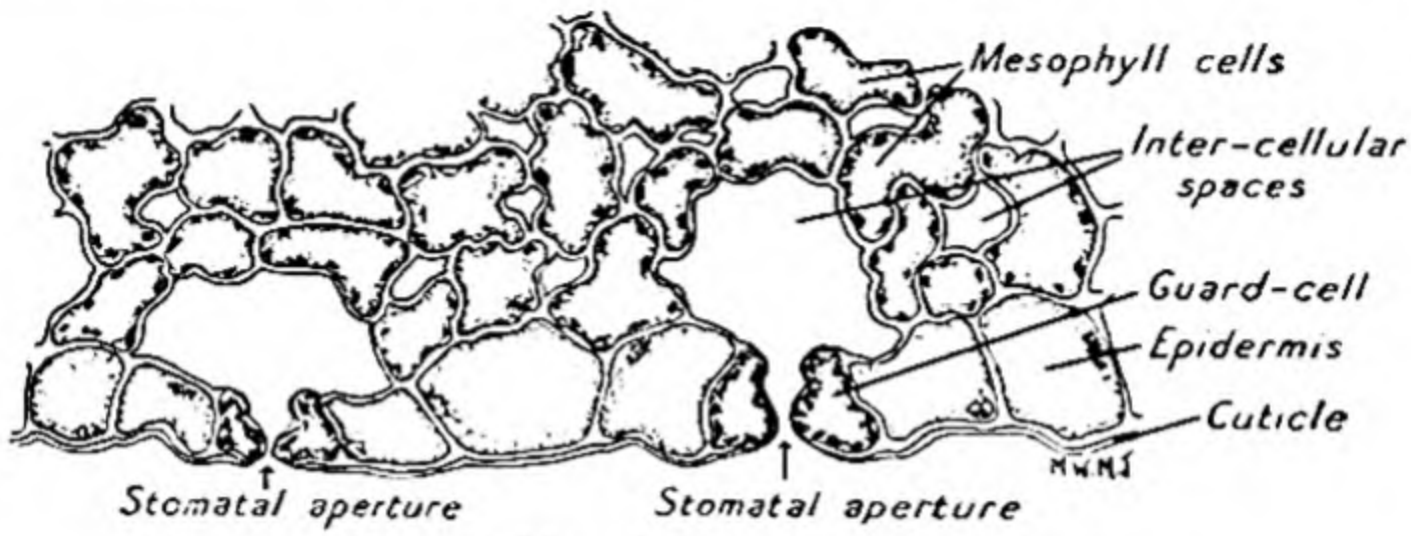


FIG. 177 – Epidermis of a leaf of *Tradescantia*.

walls are irregularly thickened. Thickening is normally at a maximum on the concave walls of the guard-cells, whilst the walls opposite to the pore remain thin. The significance of this is related to the mechanism of stomatal opening and closure, discussed on page 404. A further important feature is the possession of chloroplasts by the guard-cells, whilst these bodies are absent from the remaining cells of the epidermis.

The typical foliage leaf as represented in a mesophytic plant is very considerably modified in plants growing in abnormal conditions of water supply. These structural adaptations are discussed in Chapter 38.

Leaf-fall

Characteristic of deciduous trees is the shedding of leaves at autumn, a phenomenon of considerable importance in that the tree is assuming xeromorphic characters (page 652), whilst the resistance to wind is also appreciably decreased. The fall of a leaf is prefaced by the development at the base of the petiole of an **abscission layer**. In longitudinal section it is seen that the cells of this layer are smaller than those surrounding it, whilst its formation frequently results in a constriction being identifiable externally at the base of the leaf-stalk. The walls of this layer eventually become mucilaginous, so that attachment of the leaf to the stem is effected almost entirely by the continuous epidermis and by the vascular bundles. The leaf subsequently becomes detached, and either before or after this process a layer of cork is formed beneath the abscission layer. This is interrupted by the vascular bundle of the leaf, whilst the vessels of the bundle may be closed by means of structures known as tyloses. A **tylose** is an invagination of a pit-membrane of the wood parenchyma into the vessels. So large do they become that they appear at first sight like parenchymatous cells. The sieve tubes are closed with callus. As a result of the shedding of a leaf a triangular scar remains on the stem.

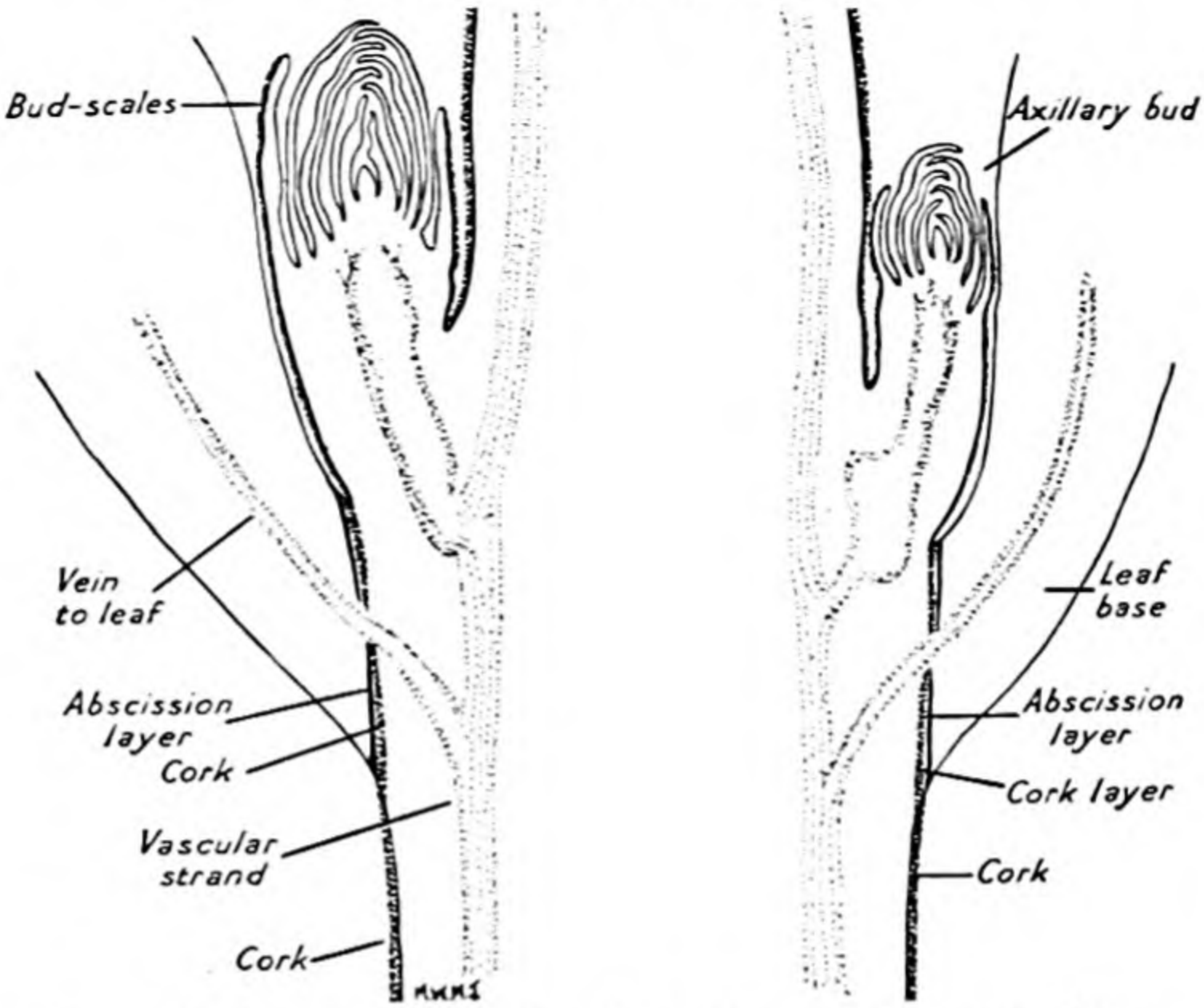


FIG. 178 – Longitudinal section of the stem of the Sycamore, showing the structural changes accompanying leaf-fall.

PRACTICAL WORK

Examine a number of leaves with a view to classifying them according to external form into simple, lobed or compound (palmate or pinnate).

Examine a number of leafy shoots and describe the arrangement of the leaves. If they are spirally arranged calculate the phyllotaxis. Sketch leaves showing different types of venation.

Examine and sketch branches of the sweet pea bearing tendrils. Notice the expanded stipules.

Examine the leaf-bases of a rose bush, noting the stipules. Examine also the spines of the gooseberry or barberry, verifying the foliar nature of the spines.

Examine as many different kinds of foliage buds as are available. Examine a prepared transverse section of a bud to discover the arrangement of the leaves within (Fig. 175B).

Cotyledons and prophylls will be examined in connexion with later chapters.

Examine a number of flower-bearing shoots, noting the structure of the bracts and bracteoles and their relation to the flower-stalks.

Cut a transverse section of a dicotyledonous leaf. In order to do this,

split vertically for about half an inch a piece of elder pith and insert the leaf in the diametric crack thus made. Cut sections of pith and leaf together. Examine under a low power in glycerine. Stain any section sufficiently thin in the manner described for the stem (page 252). Examine this or a prepared slide under high and low power. Draw very carefully.

Strip off a portion of the epidermis of a leaf of *Iris*. This may usually be done by attempting to tear a leaf slowly. Mount a portion of this colourless layer in dilute glycerol and examine to find stomata. Draw a view of one under the high-power, taking care to focus downwards so that the guard-cells are clearly seen somewhat beneath the level of the remainder of the epidermis. Examine a transverse section of a leaf of the same plant, making a very careful drawing of a stoma.

Examine and draw a prepared section showing the abscission layer and cork formed in connexion with the shedding of leaves.

CHAPTER 16

The Flower

The flower is a composite structure, specially adapted to the propagation of the species through the production of seeds. It was formerly maintained that the individual parts of the flower were essentially modified leaves. But recently palaeontological and embryological evidence has been accumulated to render this hypothesis untenable. The great antiquity of flowering plants is established, and there can be little or no doubt that the vegetative and floral parts have evolved independently. Floral organs are, in fact, to be regarded *sui generis*.

Typical Flower

Lowest on the receptacle – the tip of the flower-stalk – arise the **sepals**, usually green in colour and serving to protect the inner components when the flower is in bud. Next above these occurs an equal number of

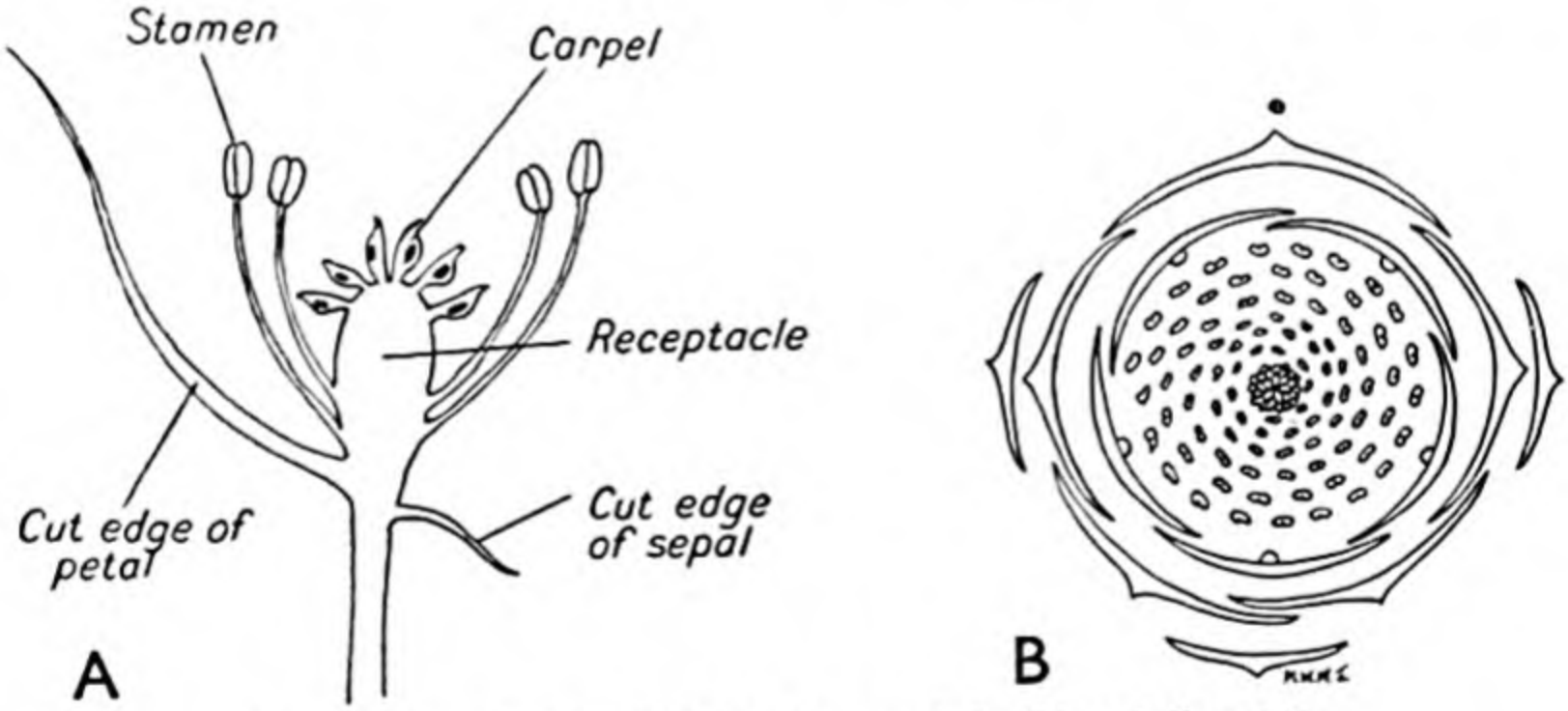


FIG. 179 – *A.*, Vertical section, and *B.*, Floral diagram, of a Buttercup.

petals, alternating with the sepals. Within and above the petals the receptacle bears a number of **stamens**. These are arranged spirally. At the apex of the receptacle arise the innermost structures – the **carpels**, arranged similarly to the stamens. This condition may be represented by means of a floral diagram, as shown in Fig. 179B. It is to be regarded as a sort of ground-plan, displaying the numbers and arrangements of parts. The main axis of the flower is shown by a dot and the side of the flower adjacent to this is described as posterior, whilst the opposite side, facing

the bract in whose axil the leaf-stalk arises (see page 258), is anterior. A line joining the mid-anterior and -posterior points is the median axis, and a vertical section cut through this line completes the diagrammatic representation of the flower. This is shown in Fig. 179*A*. This ideal condition is to some extent represented in the buttercup (*Ranunculus bulbosus*), though here the spiral arrangement is difficult to make out. It is displayed more clearly in the family Magnoliaceae, exemplified by *Magnolia* and the tulip-tree (*Liriodendron*). A more pictorial representation may be made by cutting the flower vertically in its axis of symmetry and drawing a half-flower, viewed from the cut face. Such a half-flower of the buttercup is shown in Fig. 180.

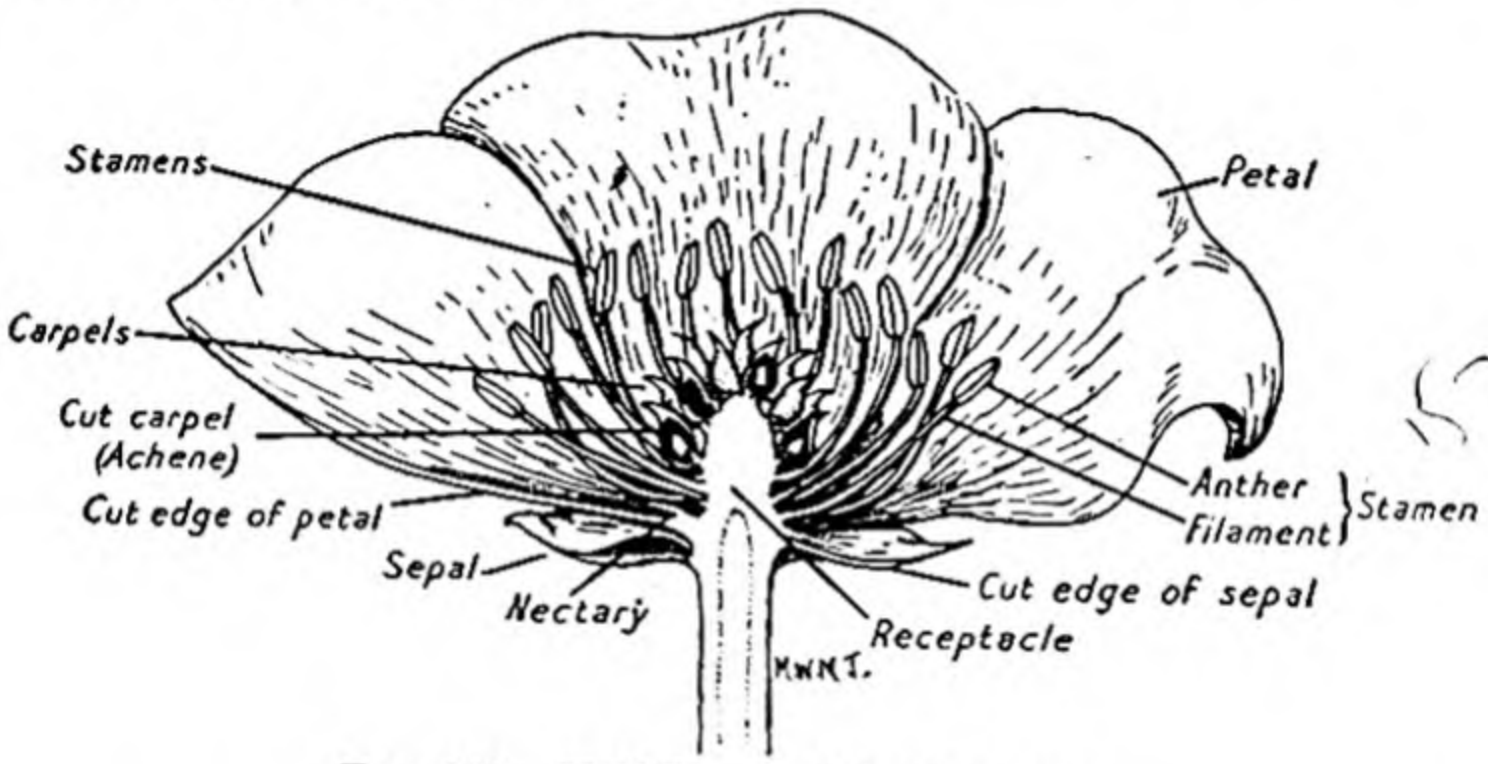


FIG. 180 – Half-flower of the Buttercup.

At this point four significant terms in floral description must be introduced. They are all of them collective terms and serve to emphasise that it is necessary often to regard each component – e.g. the petals – of a flower as a single unit of that flower. The terms in question are the **calyx** (the sepals), the **corolla** (the petals), the **androecium** (the stamens) and the **gynaecium** (the carpels). Based upon the use of these terms a *floral formula* may be compiled for any given flower. Each component is indicated by a letter – *K* (calyx), *C* (corolla), *A* (androecium) and *G* (gynaecium) – followed by a figure denoting the number of parts to that component. Thus the floral formula of the buttercup whose diagram is given in Fig. 179B would be ⊕ *K*5, *C*5, A ∞, $\underline{G}$ ∞, identical with that of the typical flower. In both cases ∞ represents a large and variable number. It should be noted that the letter *K* is used to denote the calyx in order to avoid the confusion which might arise if both calyx and corolla were represented by the letter *C*. Two further symbols here require explanation. It sometimes happens that a flower may be cut vertically in more than one plane and still give two halves which are exact mirror-images of one another. Such a flower, exemplified by the buttercup, is described as regular, or **actinomorphic**, and this condition is represented

in the floral formula by the symbol ⊕. The line drawn *beneath* the letter G indicates a superior gynaecium, whereas a line drawn *above* this letter denotes an inferior gynaecium. These conditions are explained in the following paragraph.

Modification of Floral Structure

Variations of this typical condition are brought about in a number of ways, affecting either the receptacle or the structures borne upon it, or both. In the buttercup these structures are arranged in orderly rotation on the receptacle with the gynaecium at the apex. Such a flower is described as **hypogynous**, whilst the gynaecium is said to be **superior**. A second condition is described as **perigynous**. In this the head of the receptacle has become flattened, or even invaginated. Calyx, corolla and

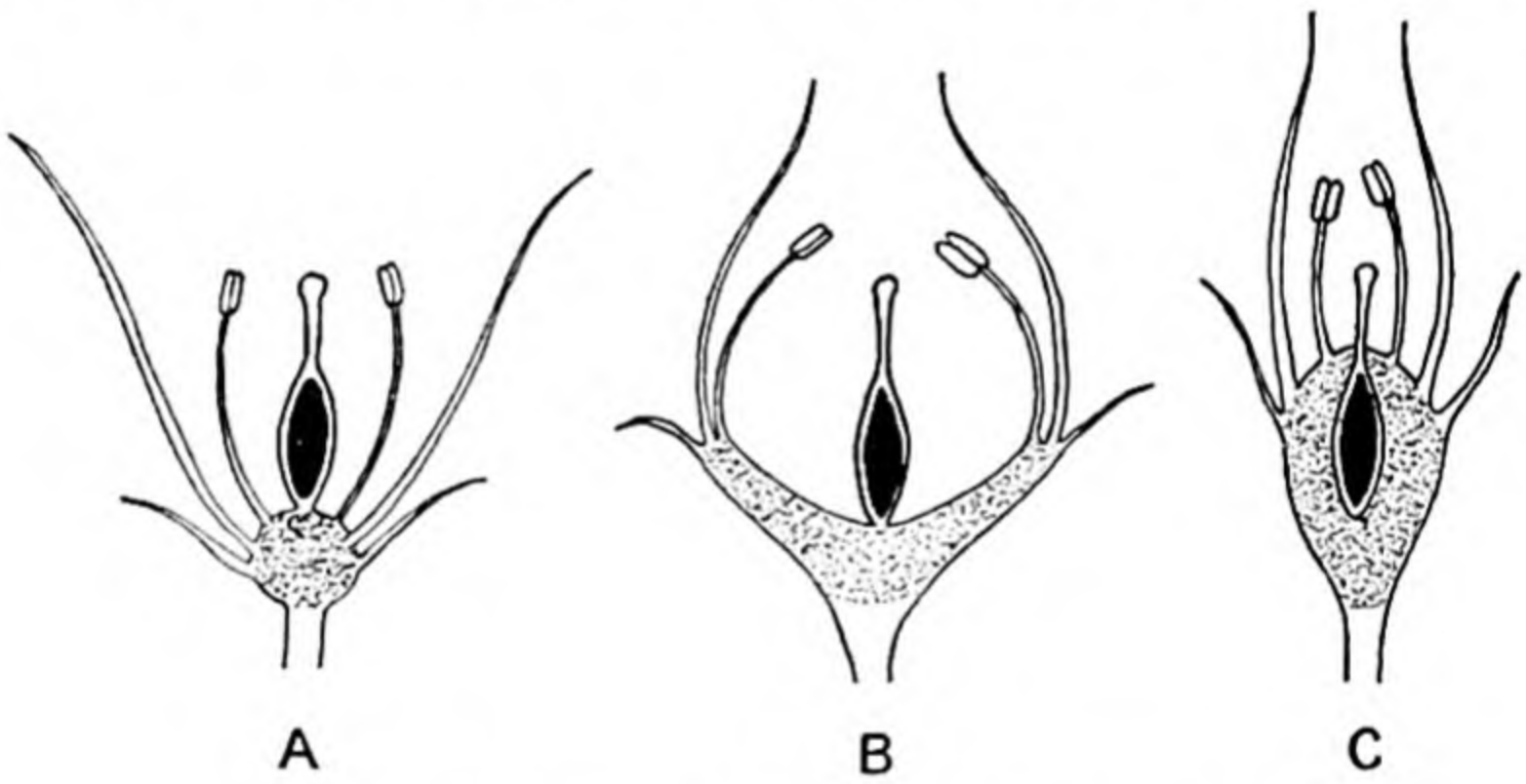


FIG. 181 – Diagrams to show types of floral receptacle.
A., Hypogynous; *B.*, Perigynous; *C.*, Epigynous.

androecium arise from the margin of the disc so formed, whilst the gynaecium originates from the base or surface of the concavity. The rose affords an example of this latter condition, whilst the gynaecium is still described as superior. A final modification is described as **epigynous**. In this form the walls of the carpels become united with the concavity of the receptacle, so that the gynaecium itself is now said to be **inferior**. Examples are afforded by *Narcissus* (e.g. the daffodil), the Umbelliferae and the Compositae.

Separate parts of the typical flower may be duplicated or suppressed. Thus in the wallflower there are two whorls of stamens, an inner of four and an outer of two. Frequently, however, stamens are absent from some flowers and carpels from others of the same species. Thus these flowers may be described as female and male respectively, as will be understood when the functions of these structures have been discussed. Catkins afford good examples of this phenomenon. Where a cluster of flowers

occurs together to form an **inflorescence** (page 273) the outer ones, as in the cornflower, may possess neither stamens nor carpels, and are hence known as neuter. Partial suppression, instead of complete, is a very common phenomenon, and the carpels particularly suffer reduction in number in many families of flowering plants.

The floral components may become partially or completely fused, either with members of the same whorl or with those of a different whorl. A common example of this is the fusion of the stamens with the petals, a condition described as **epipetalous** and seen in the foxglove.

As a result of various modifications a flower may lose its symmetry, whilst this may be retained in spite of structural changes. The typical flower described on page 264 can be divided medially into identical halves in more than one plane. It is therefore described as regular, or **actinomorphic**. This may still be possible despite the multiplication, suppression or fusion of certain parts, so that a great many flowers are actinomorphic. Others have become so modified that there is but one plane of symmetry. Such a flower is described as irregular, or **zygomorphic**. This condition is represented in the floral formula by the symbol ↑. Examples of actinomorphic flowers are provided by the buttercup and poppy, and of zygomorphic by the sweet pea and dead-nettle. On rare occasions a flower is encountered for which no axis of symmetry exists. Such are described as **asymmetrical**.

Sepals

The sepals are typically small, green leaves, as seen in the buttercup. In some forms they become petaloid – e.g. the marsh marigold and *Delphinium*. In others, especially in the Compositae (page 631), where the protective function is assumed by bracts, they become much subdivided to form hair-like structures, facilitating the distribution of fruits. This is clearly seen in the dandelion, where the calyx comprises the pappus. Occasionally there is an additional layer of sepaloid structures, outside and alternating with the true sepals. They constitute the **epicalyx**, and are believed to be formed from outgrowths of the sepals. An epicalyx occurs, for example, in the strawberry and *Geum*.

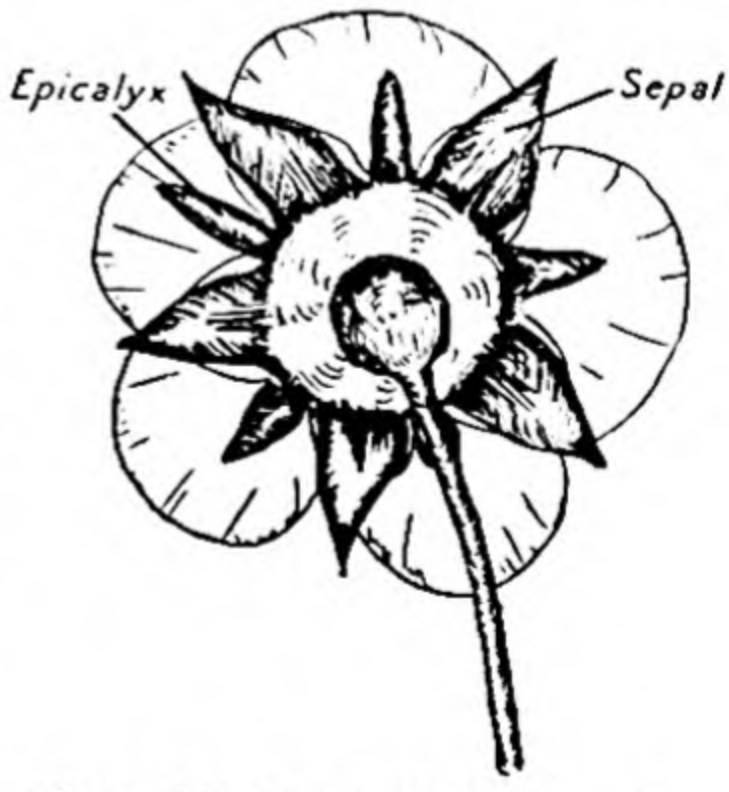


FIG. 182 – *Geum*. Back view of flower, showing the epicalyx.

Petals

The petals are very variable in form and number. They may remain separate from each other or become more

or less completely fused. In the former condition the corolla is described as **polypetalous** and in the latter as **sympetalous**, or **gamopetalous**, exemplified respectively by the buttercup and primrose. Petals are usually brightly coloured and often irregular. The petals frequently play an important part in the formation of the nectary, described on page 270. When this occurs it is usual to find on the petals lines converging towards the nectary. For this reason they are known as **nectar-guides**. The sepals and petals together constitute the **perianth**, distinct from the essential organs within, which are the stamens and carpels.

Stamens

Each stamen consists essentially of two parts – (a) a stalk, or **filament**, and (b) a head, or **anther**. Each filament is traversed by a single vascular bundle, whilst the anther is typically bilobed, each lobe normally containing two pollen sacs. Between the two lobes is a **connective**. Primitively the stamens remain free, but in other forms they become united. Thus in the gorse, for example, they constitute a tube surrounding the gynaecium (*q.v.*), whilst in the Compositae a similar tube is formed merely by the anthers, the filaments remaining separate (Fig. 343, page 633). The epipetalous condition of the stamens has already been referred to (page 267). The function of the stamens is the production of pollen.

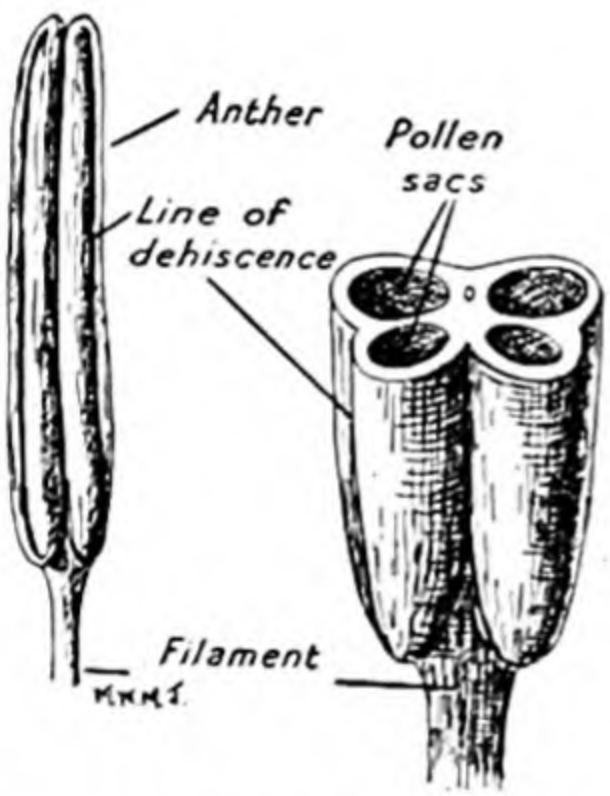


FIG. 183 – Typical stamen. *Left*, Entire; *Right.*, Cut transversely.

Carpels

A carpel is typically divisible into three parts. At the distal (free) extremity is an expanded lobe, known as the **stigma**. This is associated with the reception of pollen grains, facilitated by the secretion of a sticky fluid. At the base is the **ovary** in the form of an enlarged bulb. It contains within it the ovules, which eventually give rise to seeds, if pollination and fertilisation are completed. Connecting the ovary with the stigma is a tubular **style**.

The constitution of the gynaecium is variable. It may, as in the buttercup, consist of many completely separate carpels, in which case the gynaecium is described as **apocarpous**. In some forms, exemplified by the stinging nettle and the pea, only one carpel is present. Finally, a number of carpels may become fused together, the gynaecium being then described as **syncarpous**. In this latter case the united ovaries constitute the **pistil**, though this term is sometimes applied to the whole product of

fusion of the carpels, including the stigma and style along with the ovary. The degree of fusion is variable, extending from little more than union at the bases of the ovaries to complete coalescence to form one multiple structure.

Placentation

Each carpel bears ovules on a marginal thickening, known as a **placenta**. Hence the arrangement of these structures is termed placentation. Where the gynaecium consists of a single carpel folded so that the two edges unite the placentation is described as **marginal** (Fig. 185, A). Where several carpels become joined in the formation of the gynaecium they can do so most simply by union along their free edges. Thus the ovules will occur in rows on the walls of the ovary, giving rise to **parietal** placentation (Fig. 185, B). An advance on this condition sees each individual carpel folded, as in marginal placentation, but several such carpels become fused together with their placentae directed towards the centre of the pistil. Such placentation is known as **axile** (Fig. 185, C). If the partitions separating the cavities of the individual carpels become broken down, leaving only a central axis surrounded by the wall of the pistil, the placentation is described as **free-central** (Fig. 185, D). It is possible for this type of placentation to be

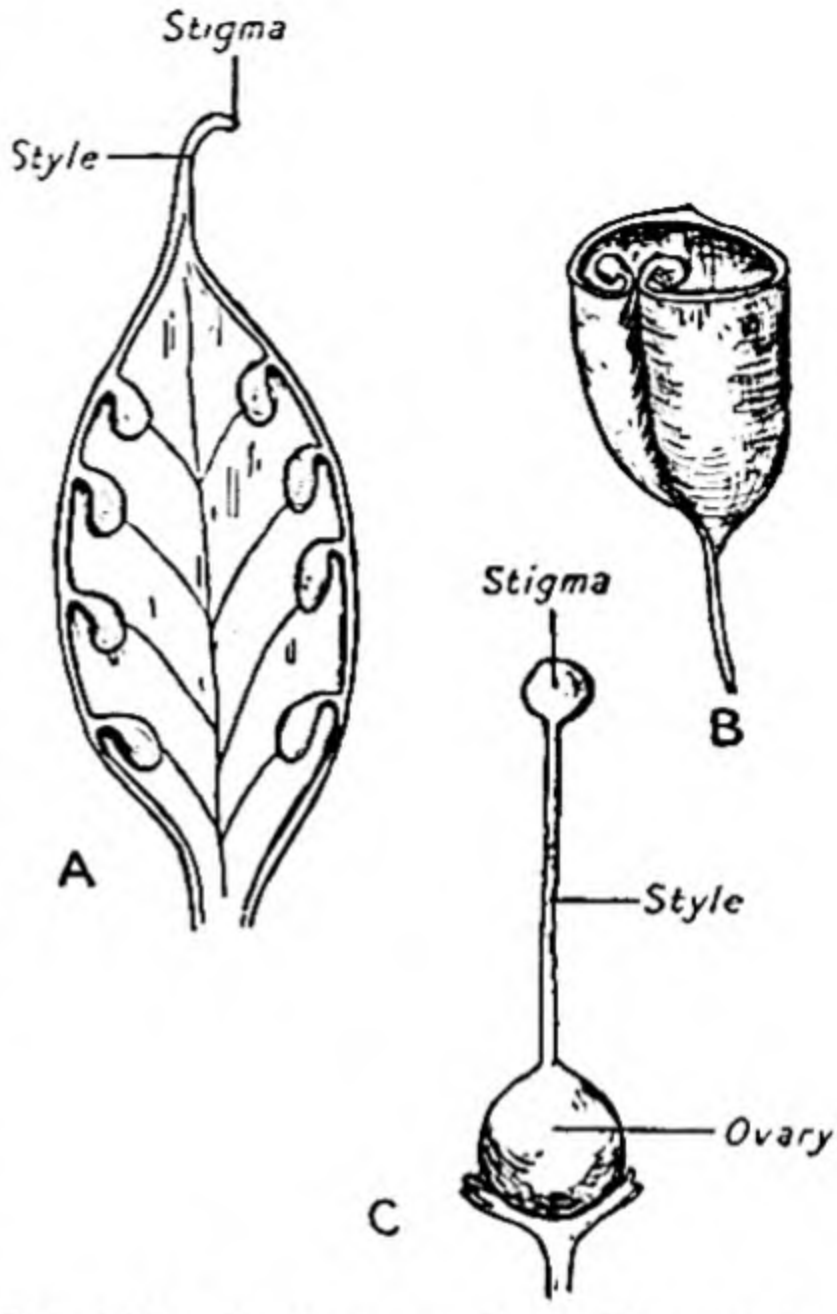


FIG. 184 – Typical carpel. A, Expanded; B, The same folded; C, The pistil

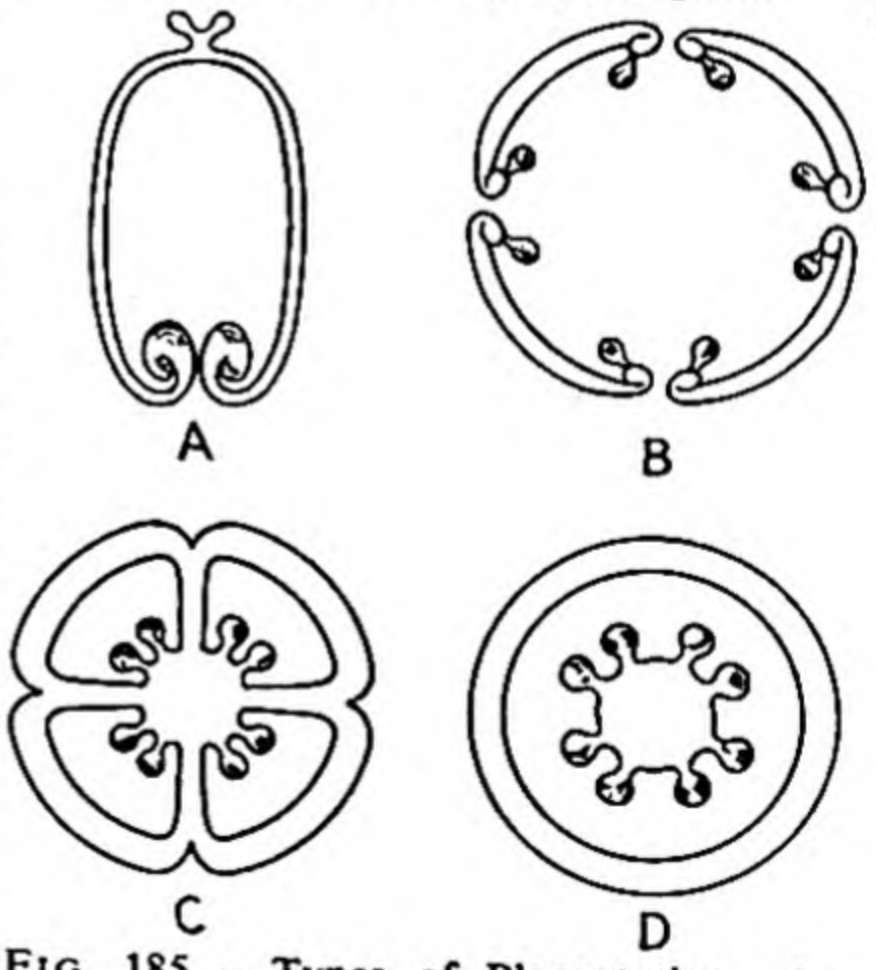


FIG. 185 – Types of Placentation. *A.*, Marginal; *B.*, Parietal; *C.*, Axile; *D.*, Free Central.

developed by the arrangement of the ovules on an extension of the receptacle passing up through the cavity of the pistil. Superficially they appear similar whichever their mode of formation.

Nectaries

Nectaries are glandular structures concerned in the production of nectar. This is collected by bees and converted to honey in the honey-stomach, afterwards being regurgitated. The form and position of nectaries in various flowers is interesting and important. In the buttercup

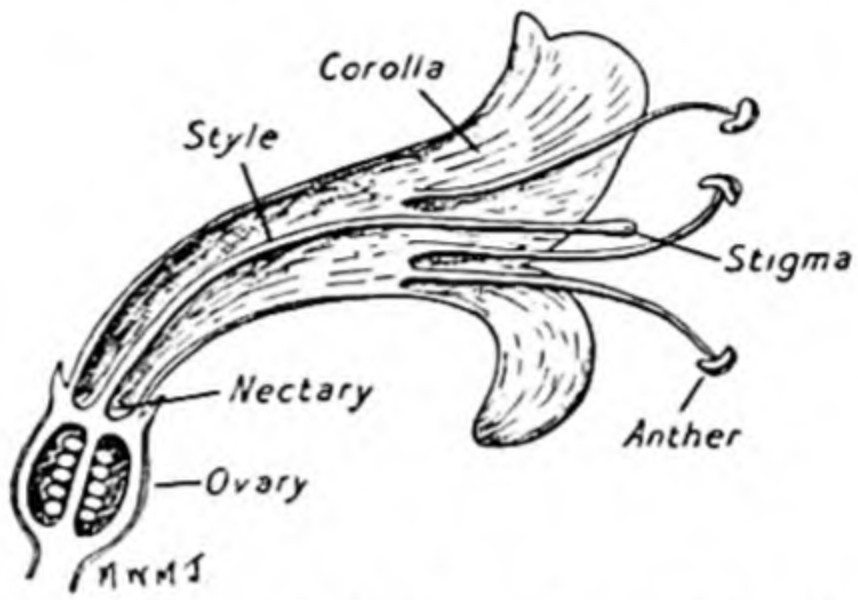


FIG. 186 – Longitudinal half of the flower of the Honeysuckle, showing the nectary.

they occur as small glands at the base of each petal, whilst in *Delphinium* the nectar is contained in the spurs projecting backwards from each sepal, being secreted by similar spurs from the petals. The production and collection of nectar in a spur is very characteristic of the orchids. Structures other than petals produce nectar. Thus, in the tulip, nectaries are situated in the walls of the ovary, whilst in the violet they occur on the stamens. In the wallflower nectaries are found on the receptacle.

In conclusion two individual flowers will be described in detail in illustration of the various general points of floral structure set out in the foregoing pages.

Buttercup

The buttercup belongs to the family Ranunculaceae, and much of its structure has already been described in the opening pages of the present chapter, to which reference should now be made. The flowers are described as hypogynous, the end of the receptacle being markedly convex. They are hermaphrodite, each bearing both stamens and carpels, and actinomorphic.

(A) CALYX. There are typically five small, green sepals, which may later become yellow in colour.

(B) COROLLA. There are five large, yellow petals, at the base of each of which is a nectary.

(C) ANDROECIUM. The stamens are numerous and free, spirally arranged on the receptacle.

(D) GYNAECIUM. The carpels are numerous, free and spirally arranged. The gynaecium is thus described as apocarpous.

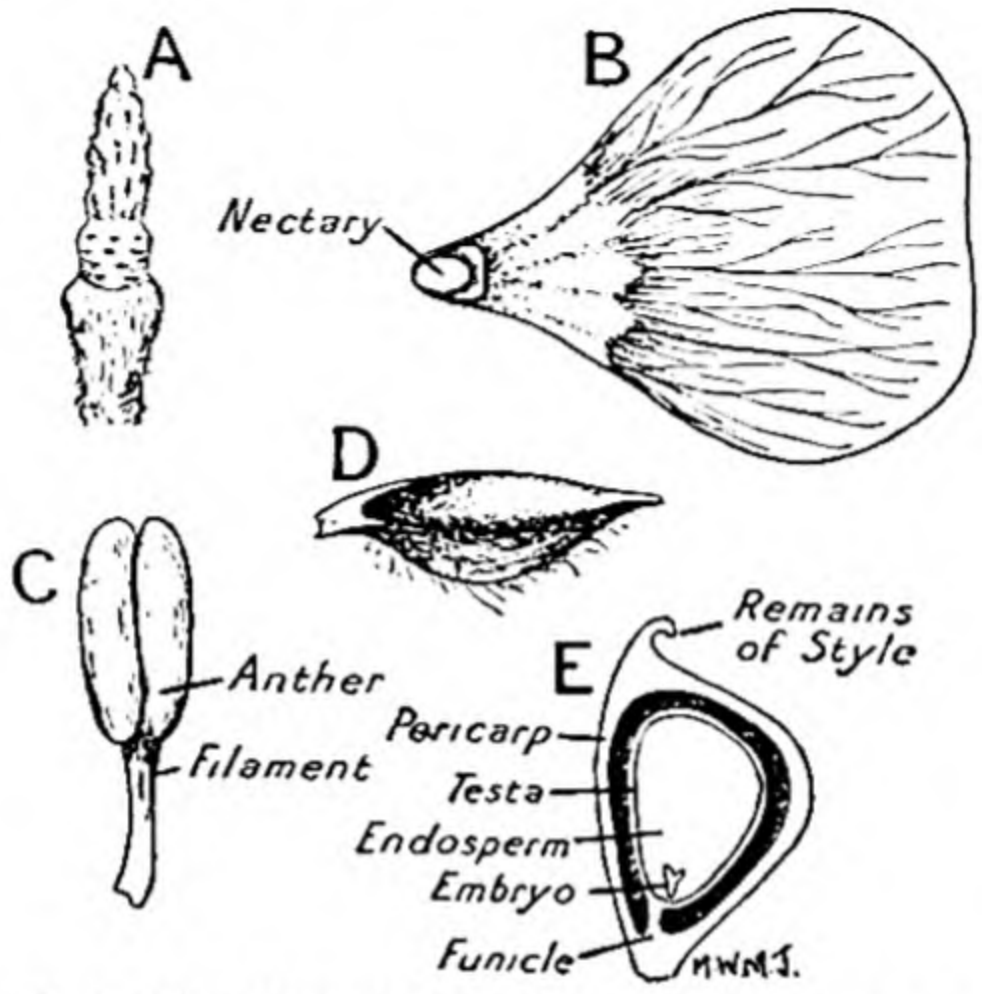


FIG. 187 – Parts of the Buttercup dissected out.
A., Receptacle; *B.*, Petal; *C.*, Stamen; *D.*, Carpel; *E.*, Longitudinal section of carpel.

Sweet Pea

This belongs to the family Leguminosae, principally characterised by the bearing of seeds in pods, or legumes. They are mentioned again in connexion with the fixation of atmospheric nitrogen (Chapter 23).

The flowers of the sweet pea are zygomorphic, hermaphrodite and slightly perigynous.

(A) CALYX. There are five sepals, more or less united, frequently in two groups, an anterior of three sepals and a posterior of two.

(B) COROLLA. The petals are peculiarly modified. There is a large posterior petal, known as the **standard**, a pair of small, lateral **wings**, and a boat-shaped structure – the **keel** – anteriorly, composed of two petals, fused at the tips and frequently for some distance along their lower edges.

(C) ANDROECIUM. There are ten stamens, nine of which are fused by their filaments, whilst the posterior one remains free.

(D) GYNAECIUM. There is one carpel, whose edges are joined at the posterior side of the flower.

Its floral formula may be represented thus: —— ↑ *K* (5) *C* 3 + (2) *A* (9) + 1 $\underline{G}$ 1.

The structure of the buttercup and the pea will be made clear by reference to Figs. 179, 180, 188 and 189.

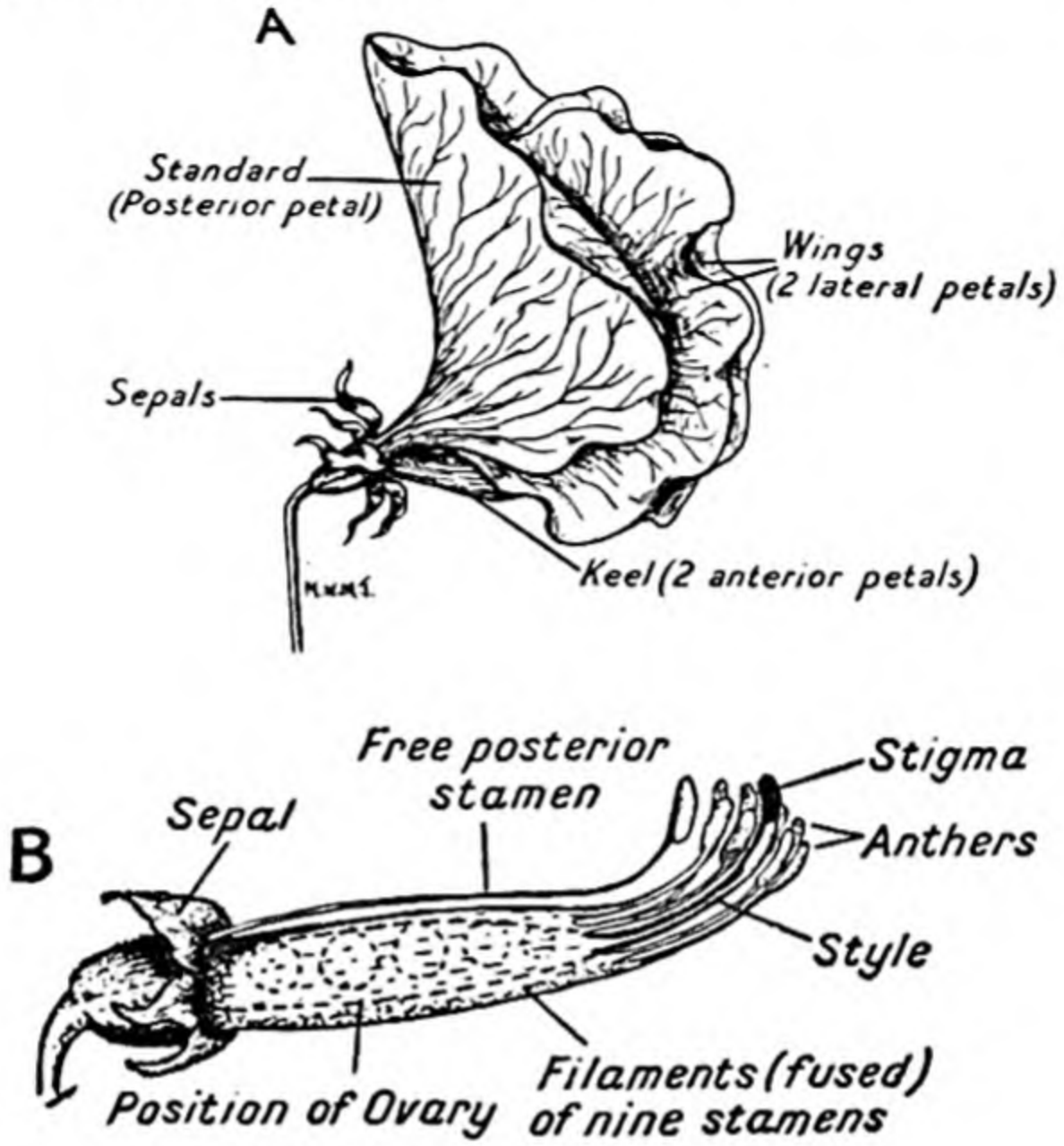


FIG. 188 – The Sweet Pea.
A., The flower from the side; *B.*, Stamens and carpel.

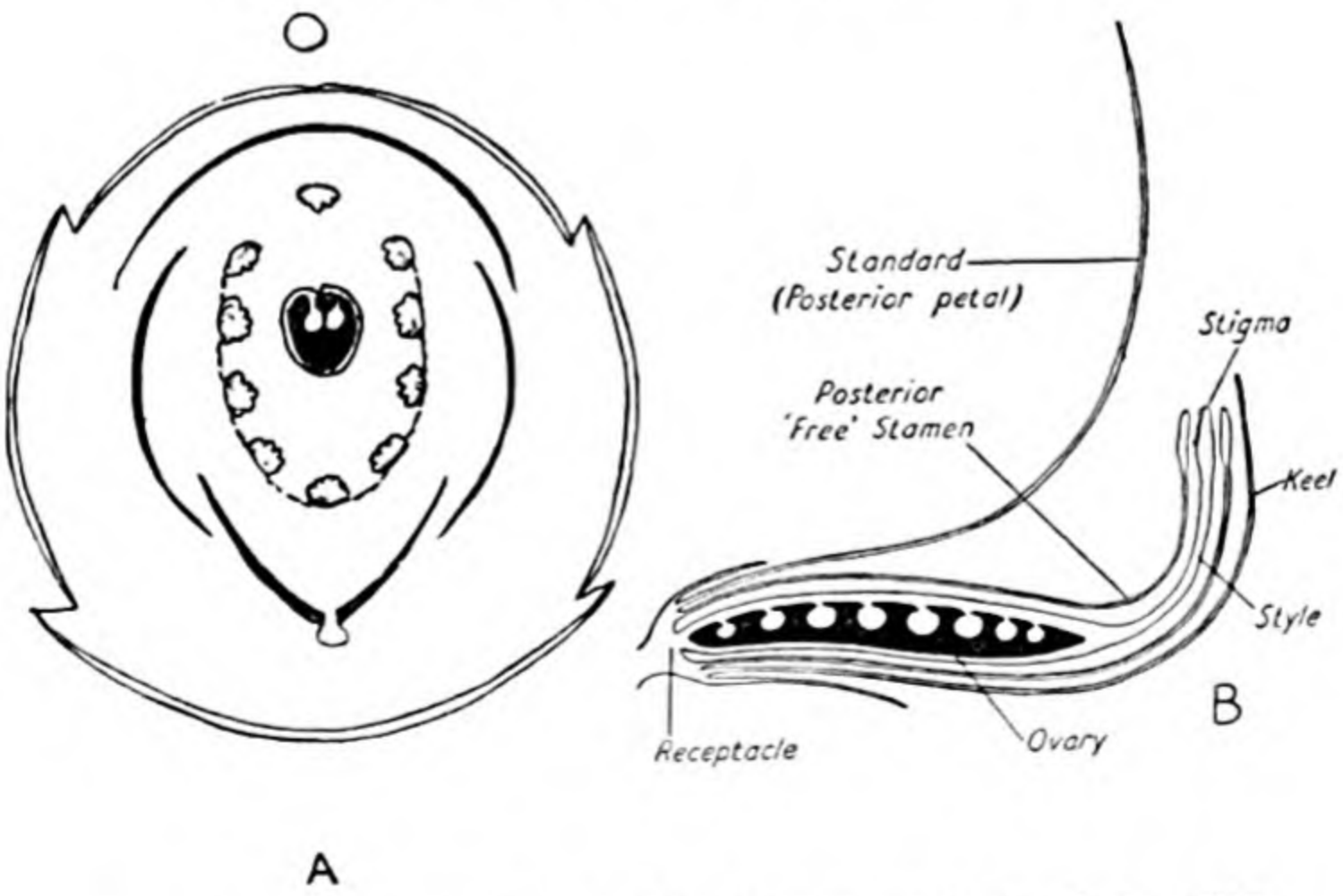


FIG. 189 – The Sweet Pea. *A.*, Floral diagram; *B.*, Vertical section.

Inflorescence

So far the structure of a single flower has been considered. It remains now to study the arrangement of flowers on the plant, together constituting the inflorescence. Flowers may be solitary, as in the tulip, though more commonly several of them are associated in the formation of an

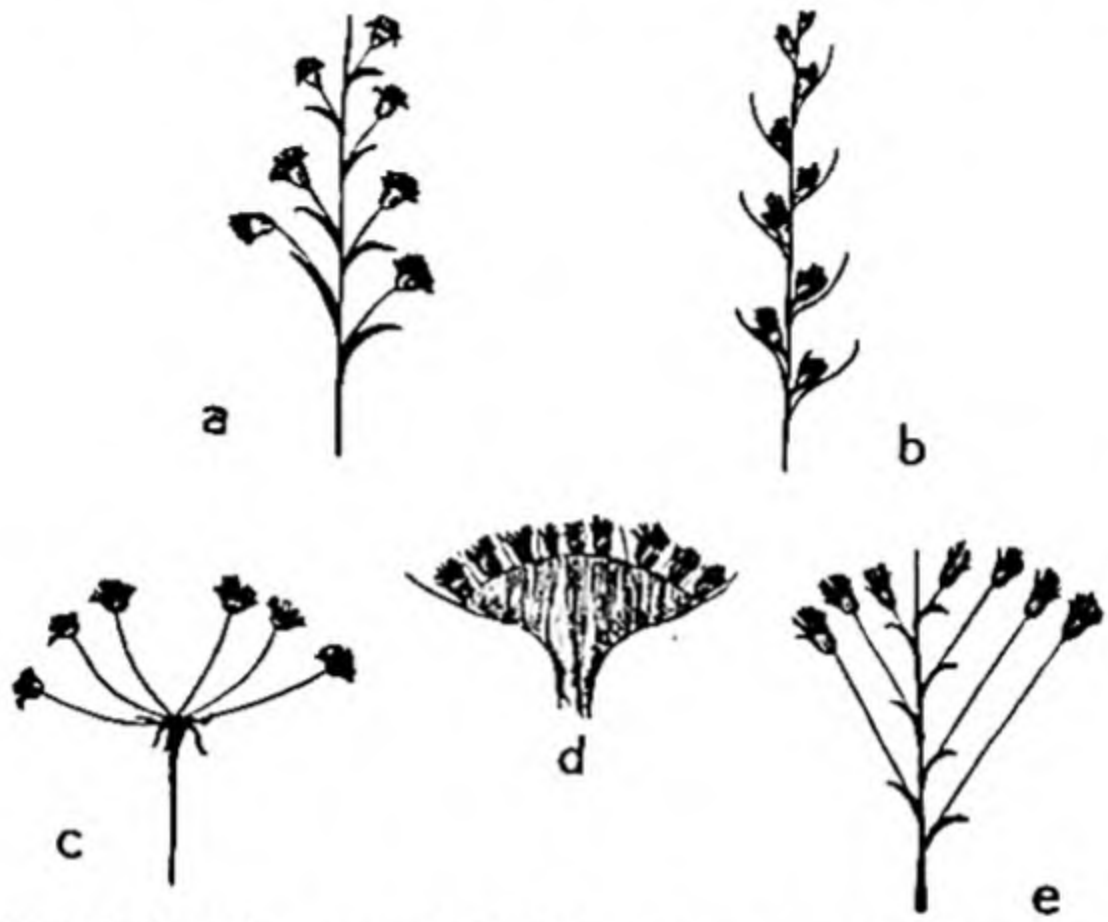


FIG. 190 – Diagrams of the Inflorescence. Racemose type.
a., Raceme; *b.*, Spike; *c.*, Umbel; *d.*, Capitulum; *e.*, Corymb.

inflorescence. If the branching of the flower-stalks is monopodial (page 242) the inflorescence is described as **racemose**, and if sympodial as **cymose**. The flower stalk is termed a **peduncle**, and the leaf in whose axil it arises a bract. Leaves borne on the peduncle are known as bracteoles. In racemose inflorescences the flowers open from the base upwards, whilst in the cymose type the reverse occurs.

(A) RACEMOSE TYPE. There are several types of racemose inflorescence, some of which are considerably modified from the typical condition.

(*a*) *Raceme.* Each separate flower has its own stalk – e.g. wallflower (Fig. 190 [a]).

(*b*) *Spike.* Flowers without stalks – i.e., sessile – e.g. plantain (Fig. 190 [b]).

(*c*) *Umbel.* A raceme in which the internodes are suppressed – e.g. cowslip (Fig. 190 [c]).

(*d*) *Capitulum.* A spike in which the internodes are suppressed – e.g. daisy and other Compositae (Fig. 190 [d]).

(*e*) *Corymb.* A raceme in which the lower peduncles are longer than the upper, so that the flowers are all borne at about the same level – e.g. candytuft (Fig. 190 [e]).

(*f*) *Panicle*. This is a compound inflorescence, consisting of an elongated main axis bearing racemes on each of many lateral branches. It occurs commonly amongst grasses.

(B) CYMOSE TYPE. The main feature of the cymose inflorescence is the termination of the growth of the central axis by the formation of a flower prior to the formation of lateral branches beneath. According to the number and distribution of these branches some sort of classification of cymose inflorescences is possible.

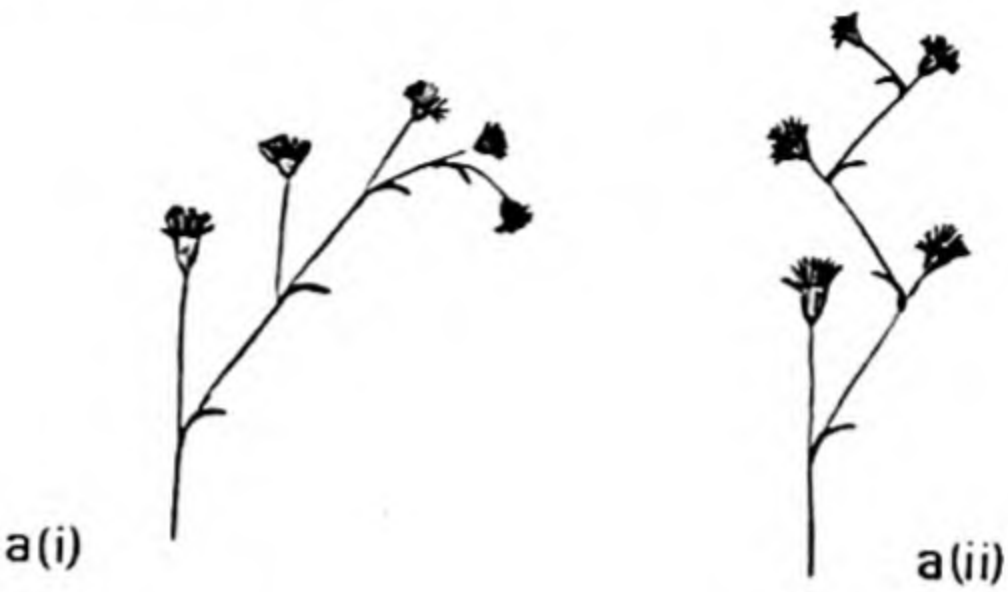


FIG. 191 – Diagrams of the Inflorescence. Cymose type.
a(i) and *a*(ii), Monochasium; *b*., Dichasium; *c*., Polychasium.

(*a*) *Monochasium*. In this type only one branch arises below the terminal flower. Each subsequent branch may arise always on the same side of the branch bearing it, as in the forget-me-not (Fig. 191 [a](i) or on opposite sides – e.g. *Iris* (Fig. 191 [a][ii]).

(*b*) *Dichasium*. In this case two opposite branches are given off below terminal flower – e.g. pinks (Fig. 191 [b]).

(*c*) *Polychasium*. This is an uncommon type in which many branches arise beneath the terminal flower – e.g. spurge (Fig. 191 [c]).

Life-history of Angiospermae

Reference has been made in previous chapters to the propagation of flowering plants by means of modified stems, both aerial and subterranean. But by far the most important method of reproduction is that dependant upon the formation and subsequent dispersal of seeds, and

for this the flower is entirely responsible. Prior to the appearance of these bodies a number of important processes occur. Both pollen grains and ovules are concerned, so that their respective developments must first be studied.

Development of Pollen

At an early stage a stamen is represented by a swelling on the floral receptacle, slightly lobulated and consisting of a mass of uniform cells, bordered by an epidermis. In each lobe of the anther there appears a rod of cells beneath the epidermis. Each rod constitutes an **archesporium** and is composed of cells with granular contents and conspicuous nuclei. By a tangential division of each archesporial cell two products are formed, the outer contributing to the wall of the pollen sac, whilst the inner divides further to form **pollen** (or **microspore**) **mother-cells**. The cells comprising the wall divide many times, so that the wall becomes several cells thick. The innermost layer is of nutritive function and is known as the **tapetum**, whilst the layer beneath the epidermis frequently becomes fibrous. Each pollen mother-cell typically undergoes two divisions, in the course of which reduction of chromosome-number from the diploid to the haploid is effected, as described in Chapter 19. Thus four pollen grains are formed, each normally contained within two coats. The outer, or **extine**, is thick and cuticularised, whilst the inner, known as the **intine**, is delicate. Pores frequently occur in the extine, and through one of them emerges the pollen tube (page 279).

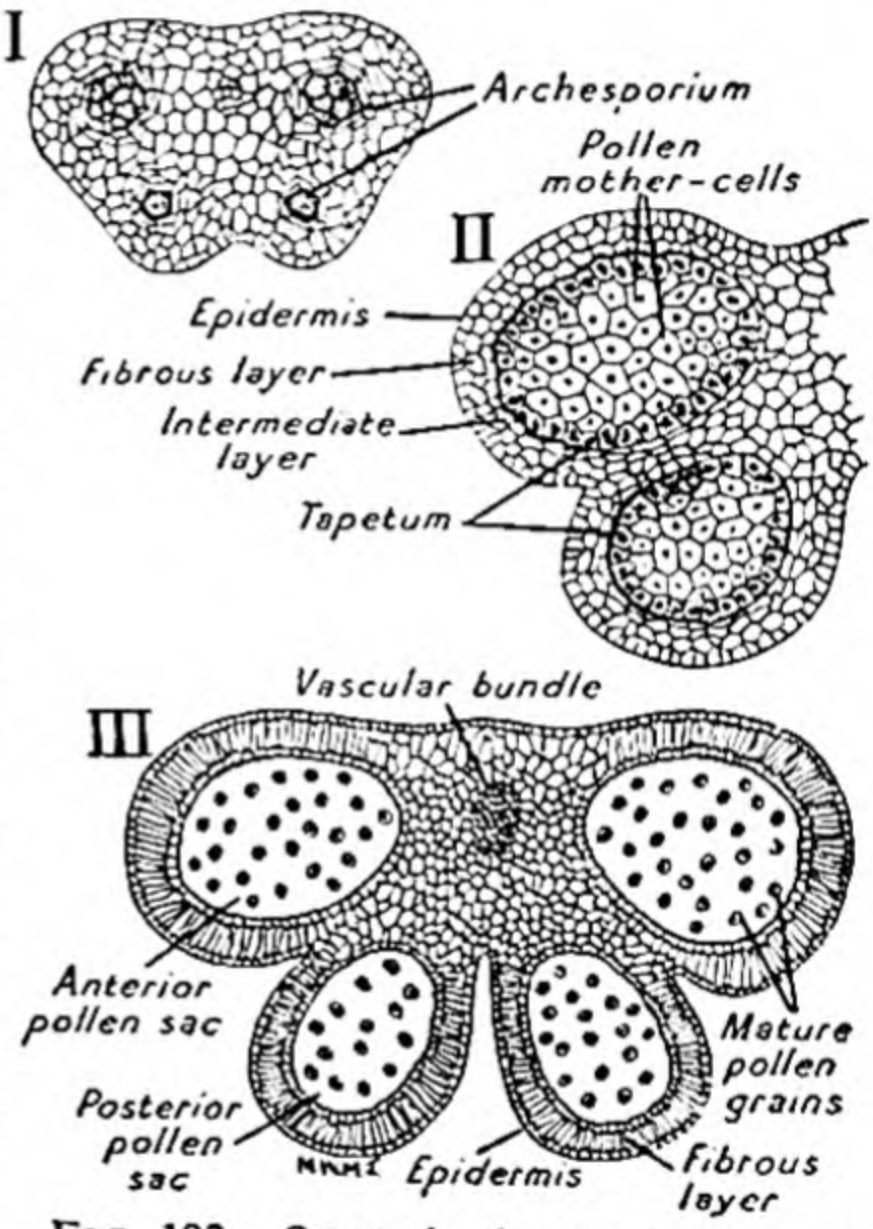


FIG. 192 – Stages in the development of the anther of a stamen.

Development of Ovule

A protuberance arises on the placenta (page 269), and the mass of cells constituting it is known as the **nucellus**. Within this a single **archesporial cell** becomes distinguishable by its large size, conspicuous nucleus and granular contents. This cell divides tangentially, the superficial product being known as the **tapetum**, whilst the inner is the **megaspore**

mother-cell. By two successive divisions, in which reduction of chromosome-number is effected, four spores are formed, arranged in a row directed inwards. The innermost becomes the functional **megaspore**, or **embryo sac**, subsequently enlarging so as to occupy most of the nucellus.

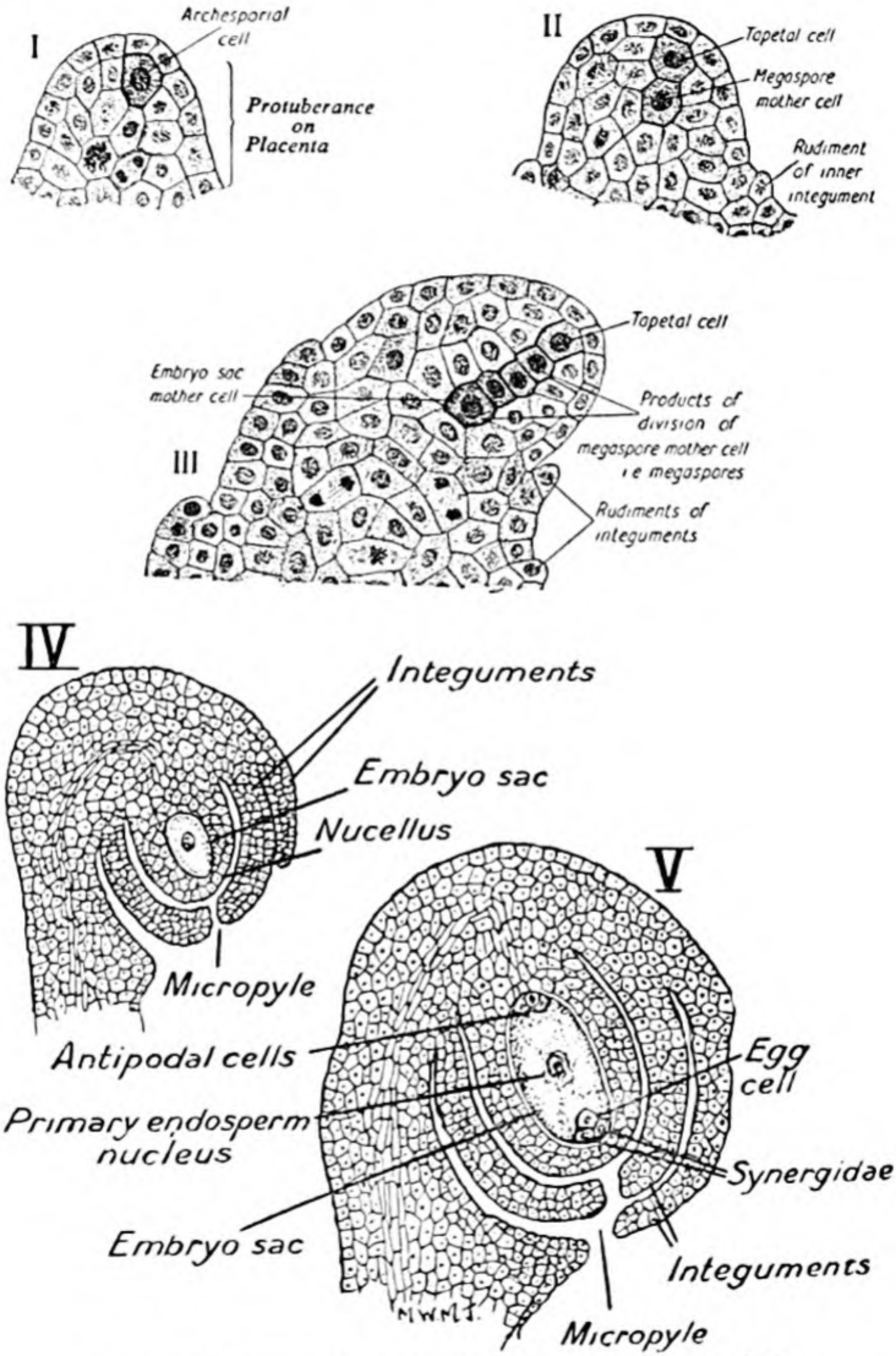


FIG. 193 – Stages in the development of the ovule of an Angiosperm.

After a while a nuclear division occurs. The two nuclei move towards opposite poles of the embryo sac, where each again divides twice, so that there are now present at each pole four nuclei, each with the haploid number of chromosomes. One nucleus from either end now returns to the centre of the embryo sac, and the two fuse, either at this stage or subsequently, to form the **primary endosperm nucleus**. Meanwhile from the base of the nucellus two cellular coats have arisen, known as the **integuments**. The inner completely encloses the embryo sac, save for a minute pore at the distal end, termed the **micropyle**. The outer integument forms a less complete investment. The nuclei of the embryo sac at the micropylar end are potential eggs, but only one becomes a mature **oösphere**, the other two being known as **synergidae**. At the end opposite the micropyle are the three **antipodal cells**. All six nuclei, as well as the primary endosperm mucleus, have an investment of cytoplasm but no cell-wall. This mature embryo sac contains the much-reduced **female prothallus**.

Pollination

Pollination involves the deposition of pollen from the stamens of one flower upon the stigma of another of the same species. Though the vast majority of flowers are hermaphrodite – i.e. contain both male and female organs – it is only on very rare occasions that a single flower will use its own pollen to pollinate its own stigma. When this does occur it is termed **self-pollination. Cross-pollination** is the rule. That pollination is essential to the production of seeds may be seen by growing plants in carefully regulated conditions in a glass-house, covered by muslin and with their own stamens carefully removed at an early stage.

Self-pollination is avoided in a number of ways. Most commonly the stamens and carpels ripen at different times. A **protandrous** flower is one in which the stamens ripen first, whilst in a **protogynous** flower the stigma is first to mature. Examples are afforded by the Canterbury bell and figwort respectively. As already mentioned (page 266) some plants bear flowers of two distinct kinds, in one of which stamens are absent and in the other carpels. Thus cross-pollination is ensured. The catkins are the commonest example of this class. In some plants – e.g. many Leguminosae – the pollen from any given flower is incapable of effecting self-pollination. This phenomenon, known as **physiological incompatibility**, is dealt with further on page 584, where the genetic explanation is outlined.

Flowers are usually either wind-pollinated (**anemophilous**) or insect-pollinated (**entomophilous**). The former produce an abundance of pollen to allow for the enormous wastage, whilst the flowers themselves are relatively simple and of sombre colour, and the pollen is readily liberated. Catkins again provide an example. Most entomophilous flowers are conspicuously coloured, whilst nectaries are usually present, resulting in

the attraction of insects. The mechanism for ensuring that a visiting insect effects pollination is often very complicated. In the Leguminosae (page 271) bees are the usual pollinating agents. A bee alights on the wings of the flower, which together form a sort of platform. As a result

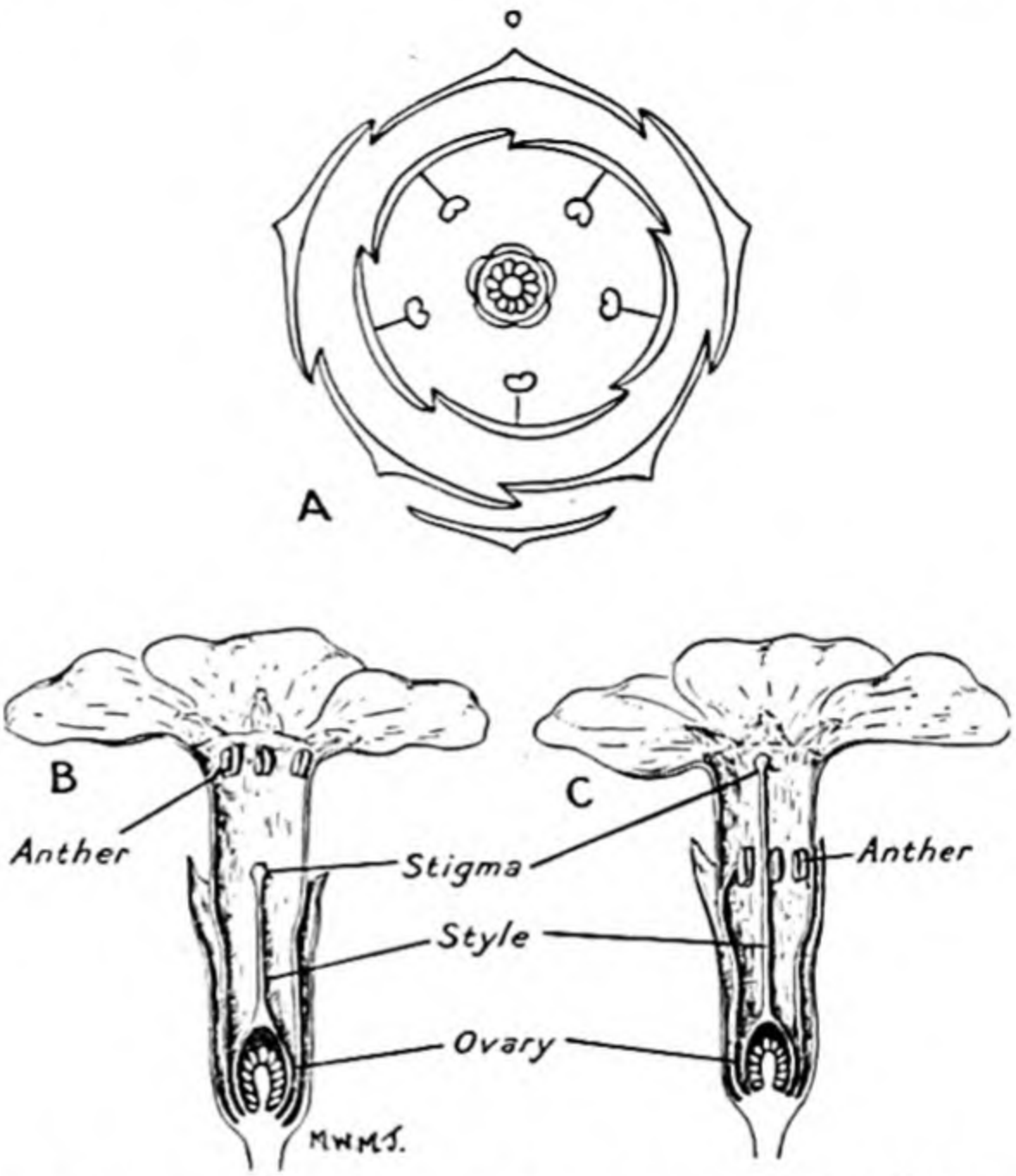


FIG. 194 – The Primrose. *A.*, Floral diagram; *B.*, Half-flower of thrum-eyed form; *C.*, Half-flower of pin-eyed form.

of the bee's weight the wings and the keel beneath it are depressed. Thus the stigma and stamens come to brush against the hairs on the under-surface of the insect's body. Pollen already present on these hairs, collected from flowers previously visited, is deposited on the stigma, whilst a fresh supply of pollen is now collected to be carried to other flowers. When the bee departs the stamens and stigma become again enclosed within the keel. Since flowers in nature are normally grouped in communities it is highly likely that an insect will travel from one flower to another of the same species many times before alighting on a flower of different species, where the pollen it carries can exert no effect. The chances of successful pollination are further enhanced by the habit of bees, for example, of collecting nectar from a particular species, passing by others on their journeys.

An interesting adaptation to cross-pollination is seen in the primrose.

There are two types of primrose, occurring in about equal numbers, one with a long style and the stamens low in the corolla tube, known as **pin-eyed**, and the other, described as **thrum-eyed**, where the style is short and the stamens situated at the mouth of the corolla tube. This constitutes the phenomenon of **heterostyly**. Consequently pollen received by an insect from the stamens of a thrum-eyed flower will be deposited immediately upon the stigma when a pin-eyed flower is visited. The pin flower also has smaller pollen grains and a rougher stigma.

The dandelion affords an interesting example of protandry in relation to cross-pollination. The anthers of the five stamens of each floret are joined laterally, thereby forming a box-like structure, through the centre of which passes the style. When the anthers are ripe the pollen is shed inwards, and at this time the style is so short that the stigma has not yet appeared above the top of the box. Furthermore the receptive surfaces of the subsequently forked stigma are, as yet, closely apposed, and the liberated pollen adheres to the hairs situated near the distal end of the style. Now the style elongates rapidly, thus carrying the stigma upwards beyond the limit of the anthers. At the same time the stigmatic surfaces become exposed, so that cross-pollination can be effected by insect visitors. Should this fail, the stigmatic prongs continue to bend backwards and curl inwards until their receptive surfaces contact any residual pollen on the style beneath them. Thus self-pollination may be effected if cross-pollination has not occurred. Reference to Fig. 343, page 630, will help to make clear the structure of a mature floret at the stage where cross-pollination is normally effected.

Fertilisation

It must be clearly borne in mind that pollination is but the preliminary to fertilisation. The two terms should not be used as if synonymous. Once a pollen grain is deposited on the stigma of a compatible flower – i.e. one on which it is able eventually to effect fertilisation – it commences to germinate. The first stage in this process has actually already occurred, for the single nucleus divides into two, one of which becomes surrounded by dense cytoplasm to form the **generative nucleus**, whilst the other, lying free within the grain, is the **tube nucleus**. A pollen tube is put out, and this penetrates the style until it eventually reaches the micropyle of one of the ovules. The tube nucleus remains near the tip of the growing tube, whilst the generative nucleus divides to form two **male nuclei**. These pass along the pollen tube in the direction of its elongation. The pollen tube eventually enters the micropyle and penetrates the nucellar cap of the ovule, thus establishing contact with the embryo sac. The two male nuclei now pass into the embryo sac. One of them fuses with the oösphere and the other with the primary endosperm nucleus. The former product of fusion, by division and differentiation, becomes the embryo plant, whilst the triple nucleus in the centre of the

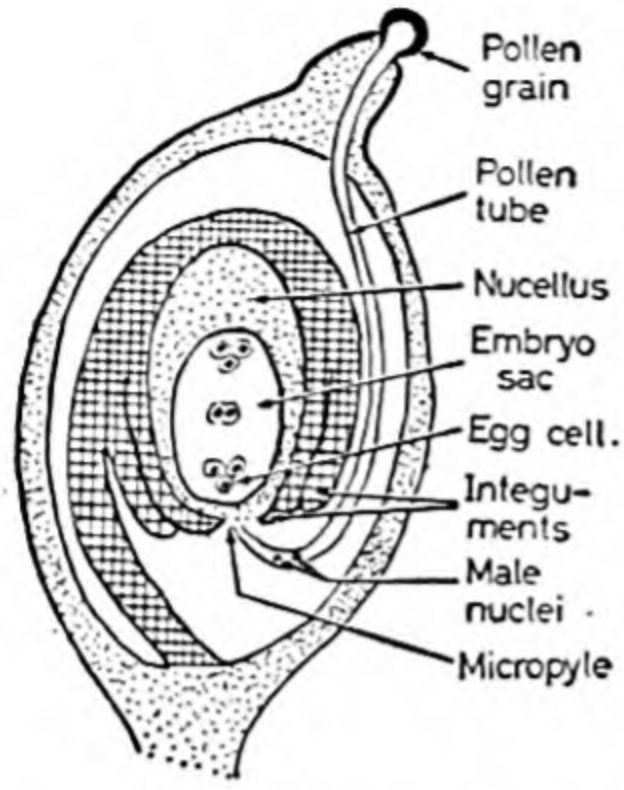


FIG. 195 – Diagram to show the path taken by the pollen tube.

embryo sac undergoes division to form a mass of nutrient material, known as the **endosperm**. In a pistil containing several ovules a separate pollen grain is essential for the fertilisation of the oösphere of each and the formation of its endosperm. Each ovule after fertilisation becomes converted into a **seed** by the modification of the integuments to form the seed coat, or **testa**, whilst the wall of the ovary enclosing all the embryo sacs forms the **pericarp**. The pericarp subsequently develops to constitute the **fruit**. The endosperm itself may be used up rapidly, so that by the time the seeds are liberated none remains. The seeds are then described as **ex-albuminous** or **non-endospermic**. Should any nucellus remain after the ripening of the seed it is distinguished from endosperm by the term **perisperm**.

Development of Embryo

The fertilised oösphere first undergoes a tangential division, and the large product nearer the micropyle plays no further part in the formation of the embryo. By transverse divisions the inner segment gives rise to a single rod of cells, known as the **suspensor**, by the elongation of which the embryo is conveyed further into the endosperm. The terminal cell eventually divides longitudinally, whilst two further divisions in planes at right angles to this result in the formation of a set of eight cells, from which the embryo plant is formed. Divisions of these cells parallel to the surface of the octants result in division into layers, the outermost of which will be the **dermatogen**, and subsequently the epidermis. The whole embryo becomes somewhat flattened, whilst the cells nearer the suspensor give rise to the **radicle**, differentiated into dermatogen and plerome. The last suspensor cell also contributes to the formation of the root-cap and periblem. At the opposite end two projections in dicotyledonous embryos constitute the **cotyledons**, between which the **plumule**, differentiated into dermatogen, periblem and plerome, arises. Since the radicle is formed at the suspensor end of the embryo it lies near the micropyle, ready for emergence. Development of monocotyledonous embryos is similar in principle, though the suspensor is usually more bulky, whilst there is but one cotyledon. Further, in dicotyledonous embryos the cotyledons are lateral and the stem apex terminal, whilst in monocotyledons the single cotyledon is terminal, the stem apex being lateral.

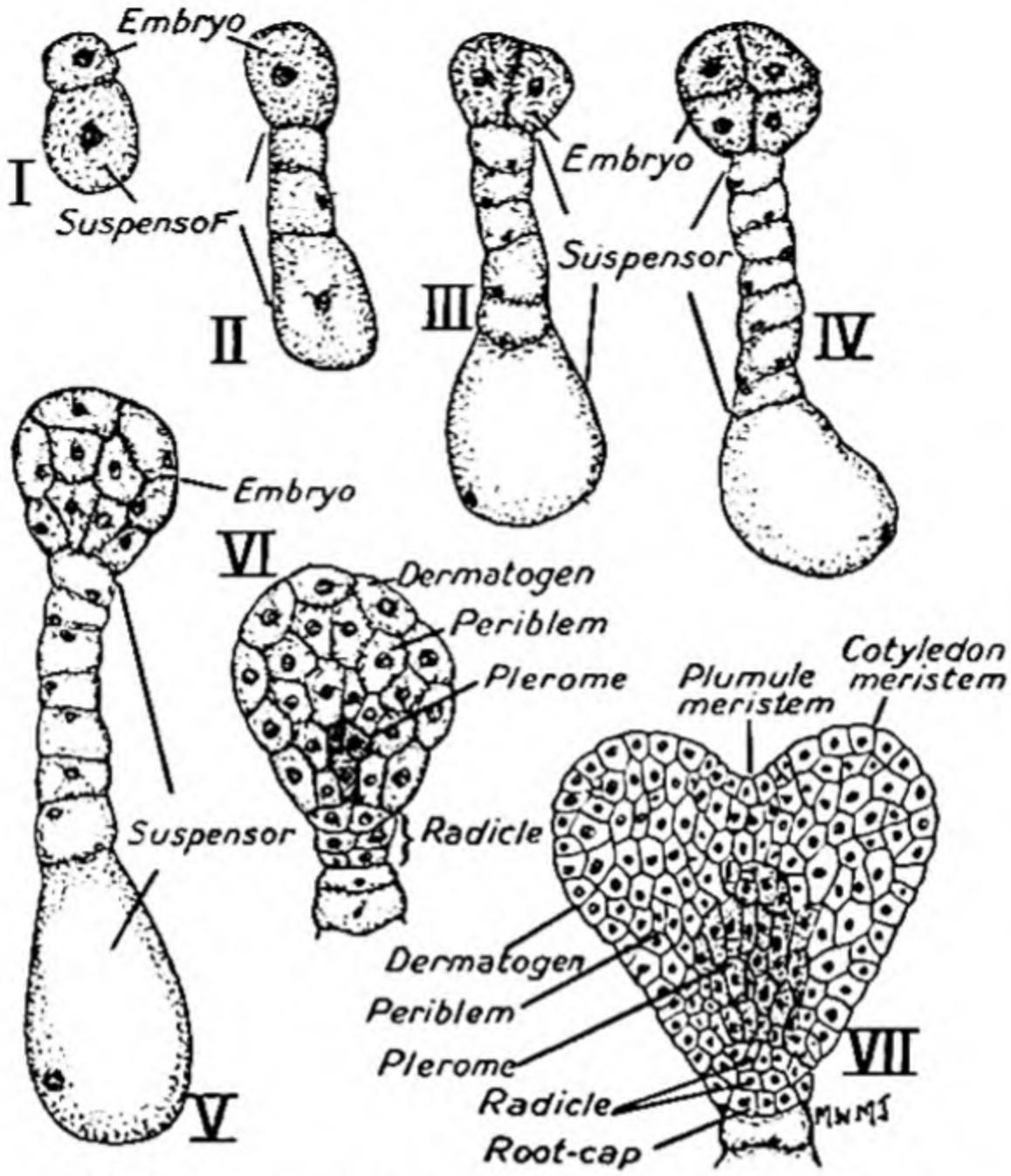


FIG. 196 – Stages in the development of a Dicotyledonous embryo.

Fruit

The essential nature of the fruit has already been noted. For convenience, however, fruits are classified according to such criteria as the number of seeds they contain, the nature of the pericarp and the number of flowers which contribute to their formation. The following classification will be found sufficiently detailed.

(A) SIMPLE. Formed from a syncarpous gynaecium.

(i) **Dry**. The pericarp remains dry.

(a) INDEHISCENT. Single seed not set free from fruit.

(α) *Achene*. The pericarp becomes tough – e.g. Compositae.

(β) *Nut*. The pericarp becomes woody – e.g. hazel nut.

(b) DEHISCENT. Many seeds, liberated from fruit.

(α) *Legume*. Fruit formed from a single carpel – e.g. the pea; or *follicle* – e.g. the marsh marigold.

(β) *Capsule*. Fruit formed from two or more carpels – e.g. the poppy.

(c) SCHIZOCARPIC. Fruit splits and each seed retains a covering of pericarp – e.g. the garden nasturtium.

(ii) **Succulent.** The pericarp becomes juicy.

(a) DRUPE. The pericarp becomes divided into three layers, namely **endocarp** (hard and woody), **mesocarp** (juicy) and **epicarp** (tough skin), e.g. plum. The seed is contained within the 'stone', the outer layer of which is endocarp.

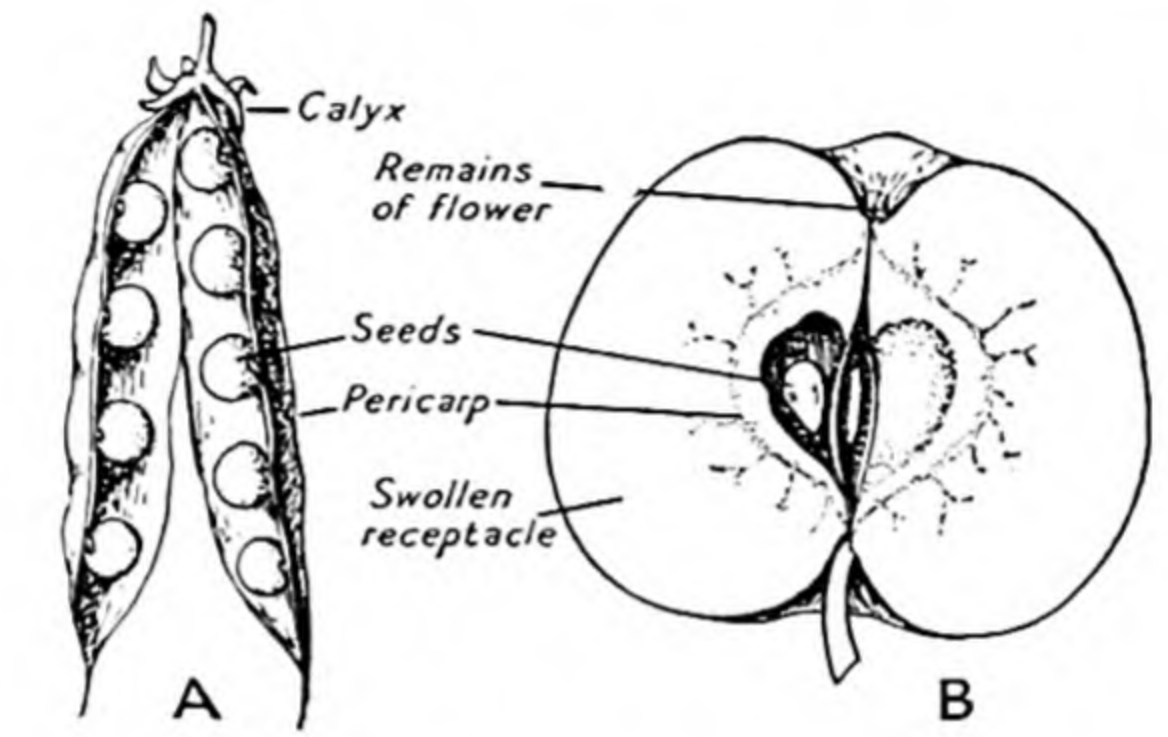


FIG. 197 – Types of fruit.
A., Legume (Pea); *B.*, False fruit (Apple); *C.*, Drupe (Plum); *D.*, Berry (Gooseberry).

(b) BERRY. The whole pericarp remains soft, except for an outer skin, and the seeds are enclosed within. A berry may be single seeded – e.g. the date – or many seeded – e.g. the tomato. If from a superior ovary the calyx is visible around the base of the stalk bearing fruit – e.g. the tomato: if from an inferior ovary at the opposite end of the fruit – e.g. the gooseberry.

(B) COMPOUND. Formed from an apocarpous gynaecium. In reality it is a collection of simple fruits.

(i) **Collection of Achenes** – e.g. the buttercup.
(ii) **Collection of Follicles** – e.g. *Delphinium*.
(iii) **Collection of Drupes** – e.g. the raspberry.

(C) MULTIPLE. Formed from a number of flowers (i.e. an inflorescence). These are mostly false fruits (see below). In the mulberry, for instance, the fruit is a collection of achenes, each enclosed within four swollen perianth lobes.

(D) FALSE FRUITS. False fruits are said to be produced when part of the flower other than the wall of the ovary contributes to their formation. The following examples should make this clear.

(i) **The apple**. Here the fleshy part is formed from swollen receptacle, whilst the core is the ovary.
(ii) **The strawberry**. The fruits (achenes) are borne on the surface of a swollen receptacle.
(iii) **The rose**. The fruits are achenes contained within the vesicular receptacle.

Dispersal of Seeds and Fruits

The fruit acts as a container for the seeds, but more important is the part it plays in their distribution. This is effected in the majority of cases by wind or by animals. Of seeds distributed by animals those enclosed in succulent fruits are obviously well adapted. Whether the fruit is true or false the fleshy portion provides food for herbivorous animals, whilst the seeds are so protected, whether by the testa or by the endocarp, that they pass unharmed through the alimentary canal of the animal, eventually being discharged in the latter's faeces some distance from the parent plant. In other cases the stone (in drupes) is not actually swallowed, but even then may get carried away for some considerable distance. Birds are amongst the commonest fruit-eaters, whilst the succulent fruits themselves are often brightly coloured for purposes of attraction. The mistletoe, growing as a partial parasite on other trees, affords an interesting example of dispersal of the seeds of succulent fruits. The contents of the fruit are mucilaginous, and on drying cause the seed to adhere to the beak of the bird. The bird subsequently rubs off this seed on the branches of another tree, so that conditions are favourable for germination.

Distribution of other fruits by animals is facilitated by the presence, either on the fruit itself or on adjacent parts of the flower, of barbed processes which adhere to the coats of animals. Consequently such a mechanism is confined to plants whose upward growth is restricted. Such barbs are formed on the wall of the ovary in the goose-grass, whilst in *Geum* the style is produced into a hooked process. Hooks may also be formed from the calyx, the involucre or on the receptacle.

Distribution of fruits by wind entails contrasted modifications of their structure. The pappus of the dandelion is formed from the calyx of each floret, whilst in the poppy the seeds are sufficiently small to be carried

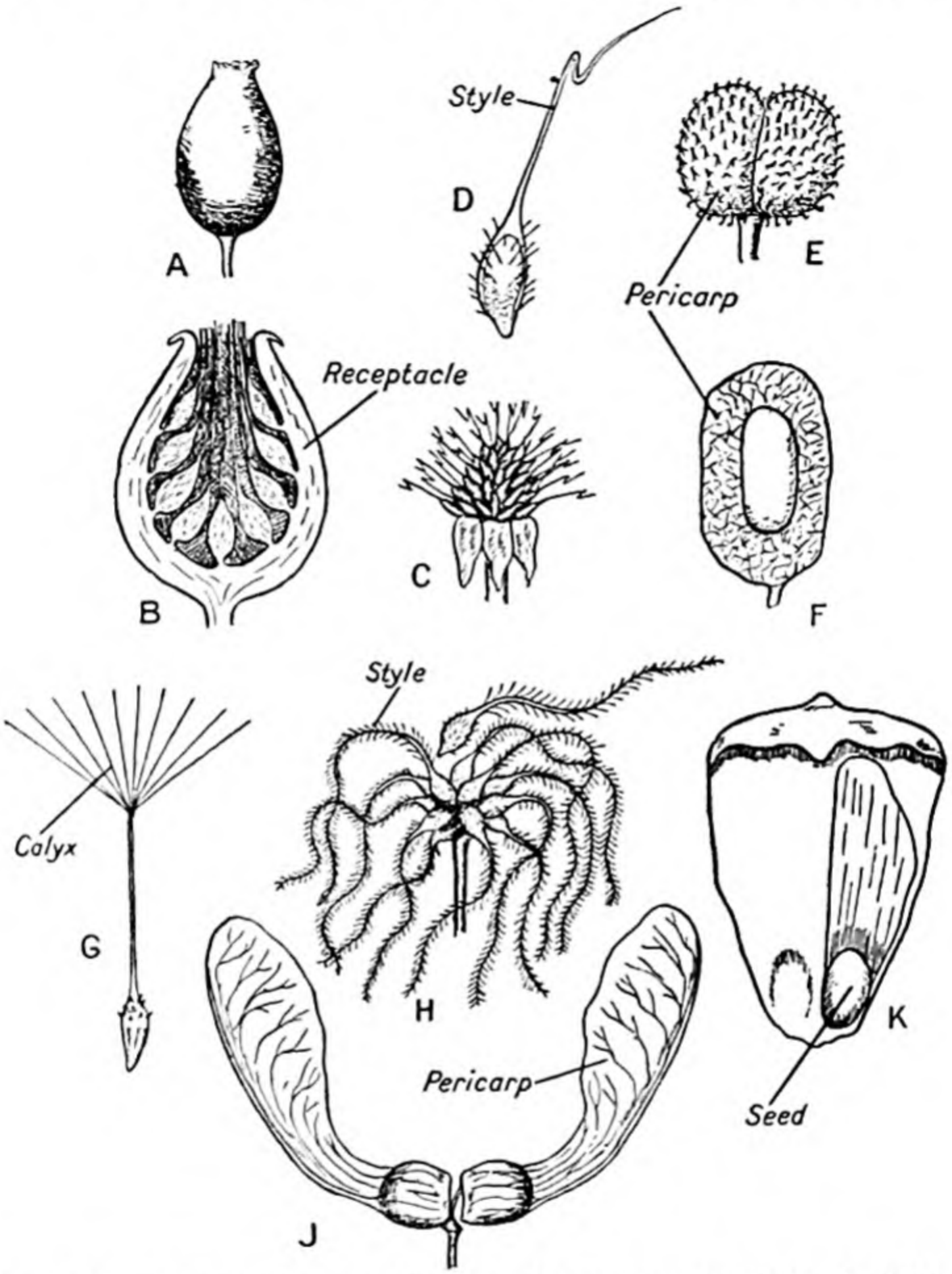


FIG. 198 – Various fruits to illustrate dispersal mechanisms. *A.*, Rose hip (entire); *B.*, The same (in vertical section); *C.*, Compound fruit of *Geum*; *D.*, A single achene of *Geum* (enlarged) *E.*, Goose-grass fruit; *F.*, Water-lily fruit; *G.*, A single achene of the dandelion; *H.*, Compound fruit of *Clematis*; *J.*, Sycamore fruit; *K.*, Seed of *Pinus*, with scale attached.

by the wind without any structural adaptation. In many-seeded fruits each seed often possesses minute hairs – e.g. the willow. In *Clematis* the hairs are borne on the elongated style surmounting each achene. Winged

fruits are exemplified by the maple and the ash. In these instances the wing is formed as an outgrowth from the fruit, but in the lime it is a modified bract. Winged seeds are comparatively rare, but examples are supplied by *Pinus* and the yellow toad-flax. In *Pinus* the wing is formed of a fragment of the ovuliferous scale.

A few fruits are dispersed by water. The commonest examples of this are the water-lily and sedges. In both cases some part of the pericarp encloses air-spaces, thus enabling the seeds to float.

Survival

Dissemination of seeds is superior to vegetative propagation as a means of survival, owing to the wider distribution thereby effected. But even so a large number of seeds will be deposited in conditions unsuitable for germination. In consequence a considerable wastage is entailed. This is overcome by the production of a large number of seeds, so that some at least may be conveyed to a favourable environment. It must always be borne in mind that upon two events depends the ultimate survival of each and every species of flowering plant. These are pollination and dispersal of seeds to positions where subsequent development may occur. In view of this it is not surprising that most plants are specially modified for the successful performance of both processes. Only a few modifications have been mentioned in the foregoing pages, but innumerable others may be discovered by the examination of flowers, seeds and fruits in their natural habitats.

Evolutionary Interpretation

Although our specific consideration of the process of evolution is reserved until later (page 590 *et seq.*), this concept must necessarily provide a background against which the great majority of biological facts are to be observed. For any type of animal or plant organism there are invariably two criteria of evolutionary success. These are the maintenance of the life of the individual through a complex of metabolic activities on the one hand, and the perpetuation of the species in time and its propagation in space on the other. The production of seeds and fruits by the flowering plant is manifestly of the greatest significance in the performance of the latter processes, and from the types studied in the foregoing pages certain conclusions may be drawn as to some of the main tendencies in floral evolution. Thus the way in which the flowers are grouped on a stalk, constituting the inflorescence, may be significant, and the massing of small flowers into compact clusters renders them more conspicuous and thus more likely to receive insect-visitors. The inflorescences of the sweet pea are racemose and of the buttercup cymose (page 274), but in both cases the number of flowers is small. But in the Compositae, though the inflorescence is racemose, so numerous are the florets and so short the internodes that the condition of extreme

compactness (capitulum) results.

Flowers regarded as evolutionarily primitive are typically regular (actinomorphic) and the successful performance of entomophilous cross-pollination thus depends rather upon the large number of parts, especially stamens and carpels, rather than upon any delicate adjustment between flower and insect. This is apparent in the case of the buttercup. But in zygomorphic flowers economy in numbers has been compensated by increased efficiency, generally through the specialisation of the corolla. This is at once apparent in the sweet pea. The effective insect-visitors must be heavy to gain access to the nectar trough, formed by the fused filaments, and must also take up a definite position, so that contact with the essential organs is assured. But the dandelion, whose pollination is described on page 279, exhibits specialisation rather in the sequence of events by which it attains sexual maturity than by structural adaptations of the individual florets. The holding aloft of the mature pollen on the hairs of the style is ideal for florets vertically held in capitula, as in this case: insect-visitors can scarcely fail to contact stigmas and styles.

A further feature of evolutionary progress is the modification of the receptacle. In its most primitive condition this takes the form of a sharply convex structure, upon which the floral components are arranged, usually in a spiral configuration, with the carpels at the apex: such flowers are described as *hypogynous* (page 266). There has been a marked evolutionary tendency for the receptacle to become first flattened, and eventually concave, with the ovaries in the latter case contained at the base. As indicated on page 266, flowers in the intermediate condition are described as *perigynous*, whilst those in which the ovary is completely enveloped within the receptacle are said to be *epigynous*. Thus progressively better protection is provided for the ovary and the climax is reached in the epigynous flowers. The buttercup is thus primitively hypogynous, the sweet pea mildly perigynous and the rose extremely so. The epigynous condition is exemplified by *Narcissus*, the apple, the Umbelliferae and the Compositae.

Evolutionary progress has also been marked by the development of fruits with characteristics essential to the dispersal of their contained seeds. These are described on page 283, and it is important to realise their evolutionary significance.

PRACTICAL WORK

Examine carefully the entire and component parts of the buttercup and sweet pea. Draw and label fully. Cut a median, longitudinal section through each. Draw. Construct a floral diagram and formula for each.

Examine carefully the receptacle and gynaecium of the rose and *Narcissus*, cutting longitudinal sections. Note that they represent perigyny and epigyny respectively, whilst the buttercup is hypogynous.

Examine and draw floral diagrams for a number of flowers, indicating their type of symmetry.

Examine and draw a number of available flowers, relating them to the description of typical and individual flowers in the foregoing chapter.

Cut transverse sections of, and examine with a hand lens (or low-power microscope), ovaries of various flowers to discover their placentation. The sweet pea affords an example of marginal, the violet of parietal, the wild hyacinth of axile and the campion and primrose of free-central placentation. Examine others and identify their placentation.

Examine the various types of inflorescence, examples of which are given in the text. Examine others and give a technical description.

Cut transverse sections of flower buds of various ages, *Ranunculus* or the tulip providing suitable material. Examine, and search for the various stages in the development of the stamens.

Examine the pollen grains from a number of flowers under the low power. Place some of the larger grains in a 2% cane-sugar solution. Examine later, when it will be found that some of them have germinated, sending out pollen tubes. Stain some of these in haematoxylin, so that the nuclear content may be observed.

Cut transverse sections of the carpel of some plant where this structure is comparatively large – e.g. the columbine. Examine until a section is found passing longitudinally through an ovule. Examine this under the high power, noting the integuments (possibly the micropyle), nucellus, embryo sac and its nuclear contents. The latter are better discerned after staining with haematoxylin. Draw.

Examine as many flowers as possible in their natural habitats. See if they are visited by insects which may effect pollination. Examine carefully a primrose (both types), sweet pea and various types of catkin. Endeavour to watch the visit of a bee to a sweet pea and primrose.

Examine a large number of fruits. Make representative sketches and notes on the various types detailed in the classification given on page 281.

Trace stages in the development of the embryo within the seeds of the shepherd's purse. This can be done by selecting seeds of various ages, when the embryo may be gently squeezed out of each. Examine under low power and draw a representative series.

Examine as many fruits and seeds as possible and determine from their structure their mode of dispersal.

CHAPTER 17

The Root

The root is that part of the plant normally, though not invariably, situated beneath the level of the ground and concerned primarily with anchorage and absorption. It may be distinguished from the stem by a number of characteristic features.

(i) Though both root and stem branch, the former never bears leaves.

(ii) The branches of a stem arise merely from the superficial layers of the axis, whilst the origin of a root-branch is much more deep-seated. This may be seen by cutting transverse sections through a stem and root in the region of origin of a branch. The branching of a stem is consequently described as **exogenous** and of a root as **endogenous**. For details see pages 248 and 294.

(iii) The tip of the stem is protected by the leaves constituting the terminal bud, but that of a root is protected by a superficial covering of cells, known as the root-cap.

(iv) The root has no chloroplasts, and thus does not appear green in colour, even on exposure to light. An exception is provided by certain epiphytic plants (page 664), where aerial roots become the organs of photosynthesis, whilst the true leaves are reduced to mere scales.

(v) The internal structure of stem and root is different.

External Structure

It has already been mentioned that the embryo plant, contained within the seed, is differentiated into radicle, plumule and cotyledons. The plumule gives rise to the shoot, whilst the cotyledon or cotyledons may become the first foliage leaves. The true root of a plant is the structure formed by the elongation and development of the radicle. In the first instance this gives rise to what is known as the **primary root**. If this persists as a central axis, subsequently becoming branched, the root is described as **tap**, whilst if the primary root becomes largely replaced by branch roots it is described as **fibrous**. Either type of root may become thickened. A swollen tap root is exemplified by the parsnip, and a swollen fibrous or lateral root by *Dahlia* and the lesser celandine. The root-nodules of the Leguminosae are described in Chapter 23.

A root is observed to become progressively thinner away from the part nearest the base of the stem. Covering the tip of the root is a **root-cap**. This may best be seen by examining under the low power an entire root from a young seedling. A short distance behind the root-cap is a region

bearing delicate outgrowths, known as **root-hairs**, whilst these are absent from the thicker (older) parts. They are concerned with the absorption of water and mineral salts from the soil (Chapter 22). In this connexion it is interesting to notice the relationship between the type of root and the disposition of leaves. In a plant with a tap root rain-water is directed inwards towards the centre of the plant, as seen in the carrot or parsnip.

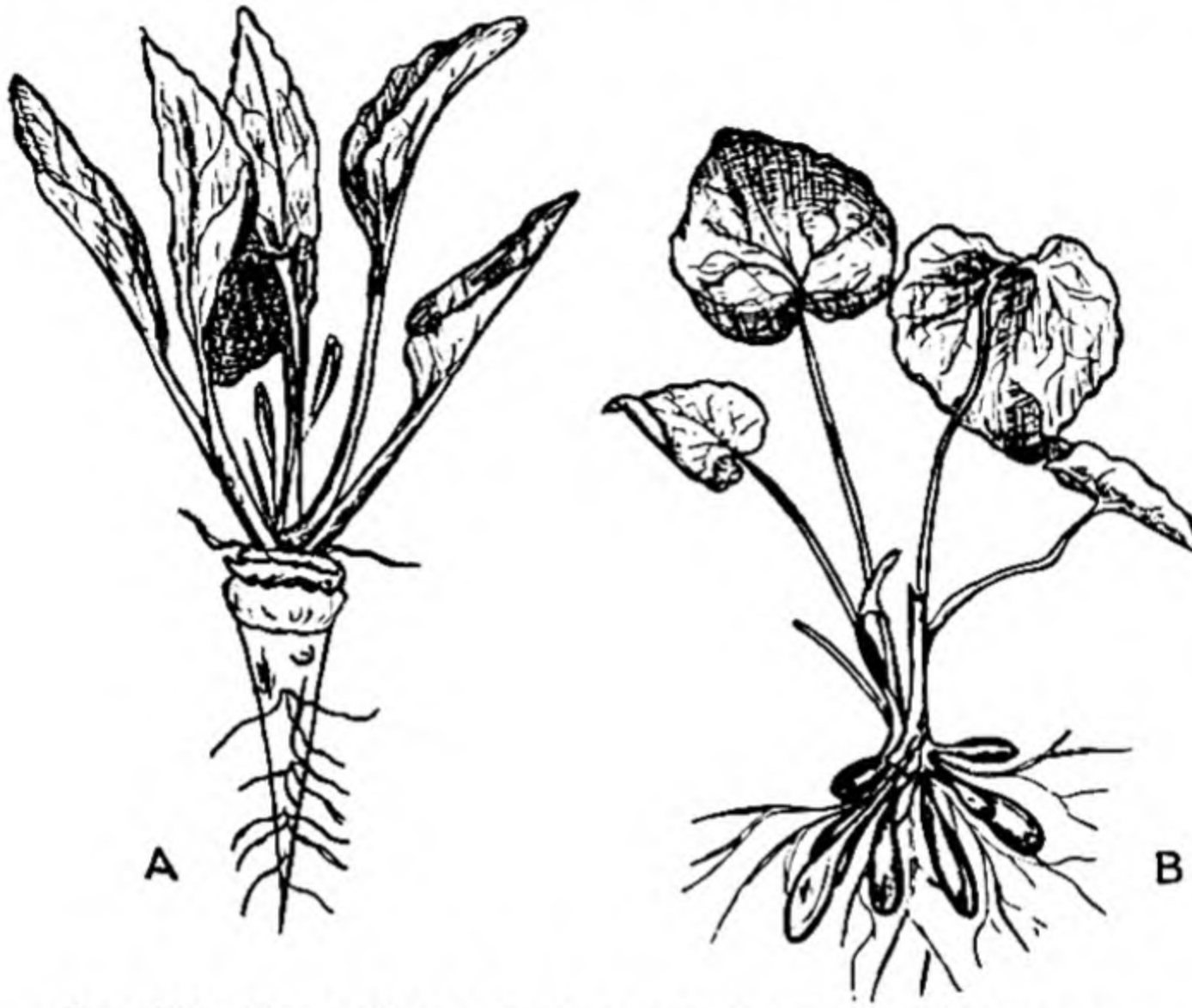


FIG. 199 – Types of root. *A.*, Tap root; *B.*, Tubercled fibrous root.

This is probably due to the usual possession by biennials of a large terminal bud. Where a fibrous root is present rain-water is conveyed to the outer edge of the plant before finally falling to the ground. In both cases, therefore, it reaches as nearly as possible the region of maximum absorption.

Adventitious Roots

Not all roots are derived from the radicle of a seed. Those arising in any other way are described as **adventitious**. They are normally developed from stems, the most obvious example being afforded by their origin from bulbs, corms, rhizomes and tubers, as well as from various creeping stems (page 240). In *Begonia* they arise from the leaves.

Functions of Roots

The functions of roots are three-fold. They are (i) Anchorage, (ii) Absorption and (iii) Storage.

In accordance with its serving for attachment of the plant the upper

portion of the root becomes thickened and strengthened. The young tips of the roots retain their delicate structure, absorption being accommodated by the root-hairs. Roots frequently become distended with reserve food material. An important group of plants of which this is a common characteristic are the **biennials**. Starting from a seed, this germinates and in its first year of life a foliaceous plant is produced, which, however, does not bear flowers. At the end of the growing season nourishment is concentrated in the root, which becomes distended. It remains dormant through the winter, and in the following spring a new shoot arises, absorbing the stored food from the root. This bears flowers, which may be pollinated, and eventually seeds are produced and dispersed. The plant then dies. Thus the term 'biennial' refers to its duration of life, occupying two years. All the so-called root-crops afford obvious examples of biennials – e.g. carrot, turnip and beetroot. In contrast the **annuals** germinate from seeds, develop flowers and set seed all in one season. **Perennials** survive in one of two ways for a number of years. Trees and shrubs are characterised by the storage of food in the woody portion at the end of the flowering season, whilst leaves of deciduous trees are shed. With the advent of spring the food is redistributed to the regions of growth. Perennials also propagate themselves by means of underground stems, as described on page 240. The obvious difference is that with trees and shrubs the skeletal architecture remains essentially the same between one season and the next, whereas plants propagated by underground stems must needs develop a new shoot at each season.

Internal Structure

As with the stem it will be found convenient to describe first a young dicotyledenous root, then to note the differences exhibited by a monocotyledonous root, and finally to describe the process of secondary thickening.

Young Root

The outermost layer in the region of the tip may be seen in transverse section to consist of a single row of thin-walled cells, many of which are produced laterally to form hollow outgrowths. These are the root-hairs, and the layer is consequently known as the **piliferous layer**. It corresponds to the epidermis of the stem, but above the root-hair region its cells shrivel and eventually die off. In this older part of the root the outermost layer consists of a row of thickened cells, constituting the **exodermis**. The cells are suberised (page 305) and are thus impermeable to water. Within the exodermis lies the **cortex**, consisting of large, parenchymatous cells enclosing a certain amount of air-space. The cells themselves contain numerous starch grains. The cortex is limited on its inner side by the **endodermis**, consisting of a single layer of cells, whose walls, especially those in a radial position, are considerably thickened. As in

the stem a **pericycle** occurs within the endodermis, the two layers together closing off the **stele** from the cortex. Within the stele are the vascular elements. The **xylem** and **phloem** are arranged in alternating bundles, a distribution described as radial, in contrast to the collateral arrangements in the stem, where xylem and phloem occur on the same radii.

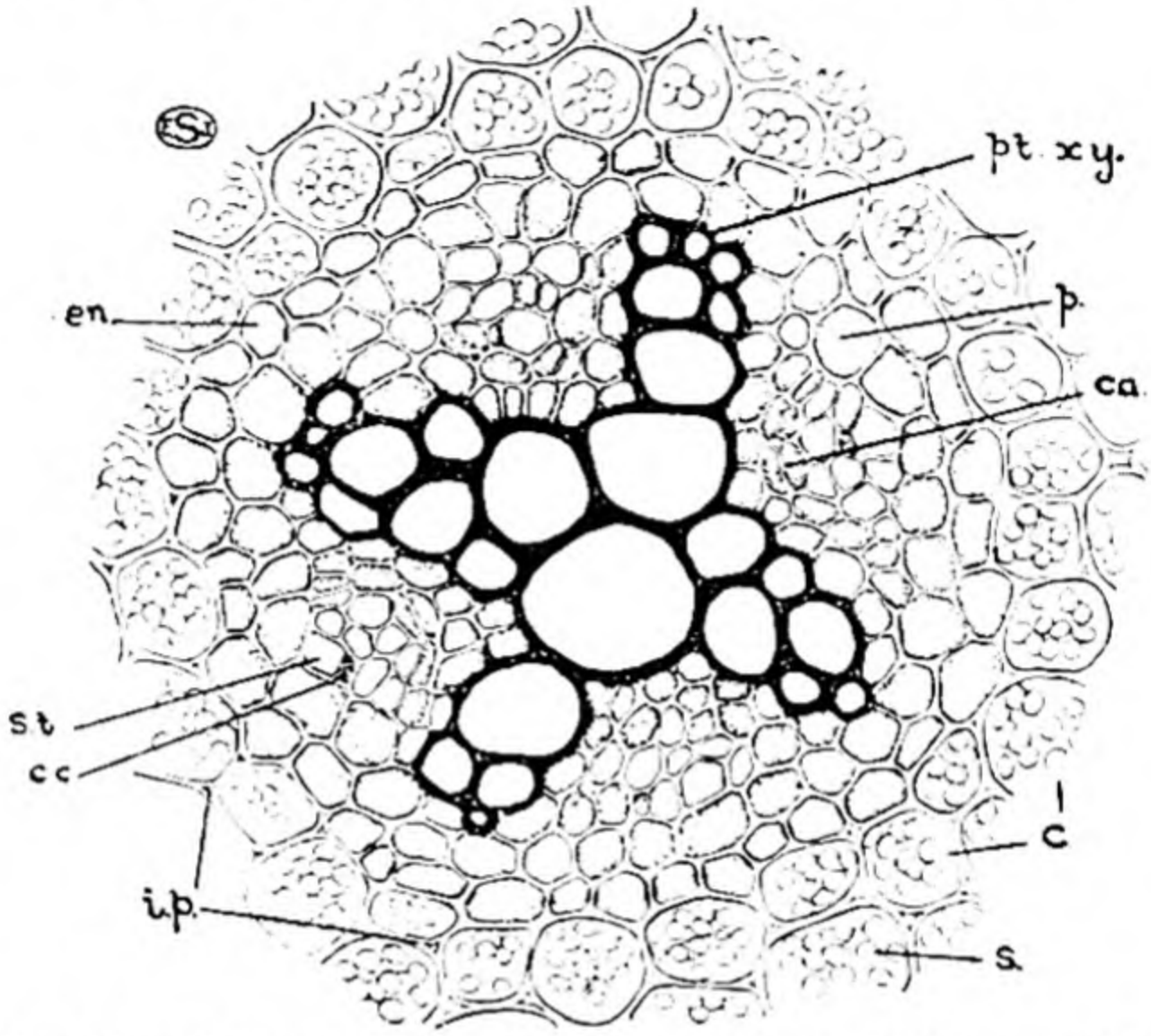


FIG. 200 – Transverse section of the central part of the root of the Creeping Buttercup (*Ranunculus repens*). The walls of the xylem elements are shown black. (From 'Plant Form and Function', by F. E. Fritsch and E. J. Salisbury. Bell.)
c., inner part of cortex; *ca.*, parenchyma; *c.c.*, companion cell; *en.*, endodermis; *i.p.*, intercellular spaces; *p.*, pericycle; *pt.xy.*, protoxylem; *s.*, starch; *s.t.*, sieve tube.

According to the number of patches of xylem and phloem present in section the root is described as di-, tri-, tetr- or pent-arch. The xylem extends inwards almost or completely to the centre of the root, the protoxylem consisting of smaller elements than the metaxylem and occurring towards the periphery of the stele (cf. the stem). The phloem consists of much smaller cells, fairly readily distinguishable into sieve tubes and companion cells (page 339).

Monocotyledonous Root

The monocotyledonous root is quite similar to that of a Dicotyledon. There are usually many more bundles of xylem and phloem present, so that it is described as polyarch. The cells between the bundles are fibrous, whilst the cells of the endodermis have their tangential, as well as their

radial, walls thickened. Accordingly the transfer of water through this layer is facilitated by the presence in it of unthickened **passage cells.** No cambium is formed, nor does secondary thickening occur. In the centre

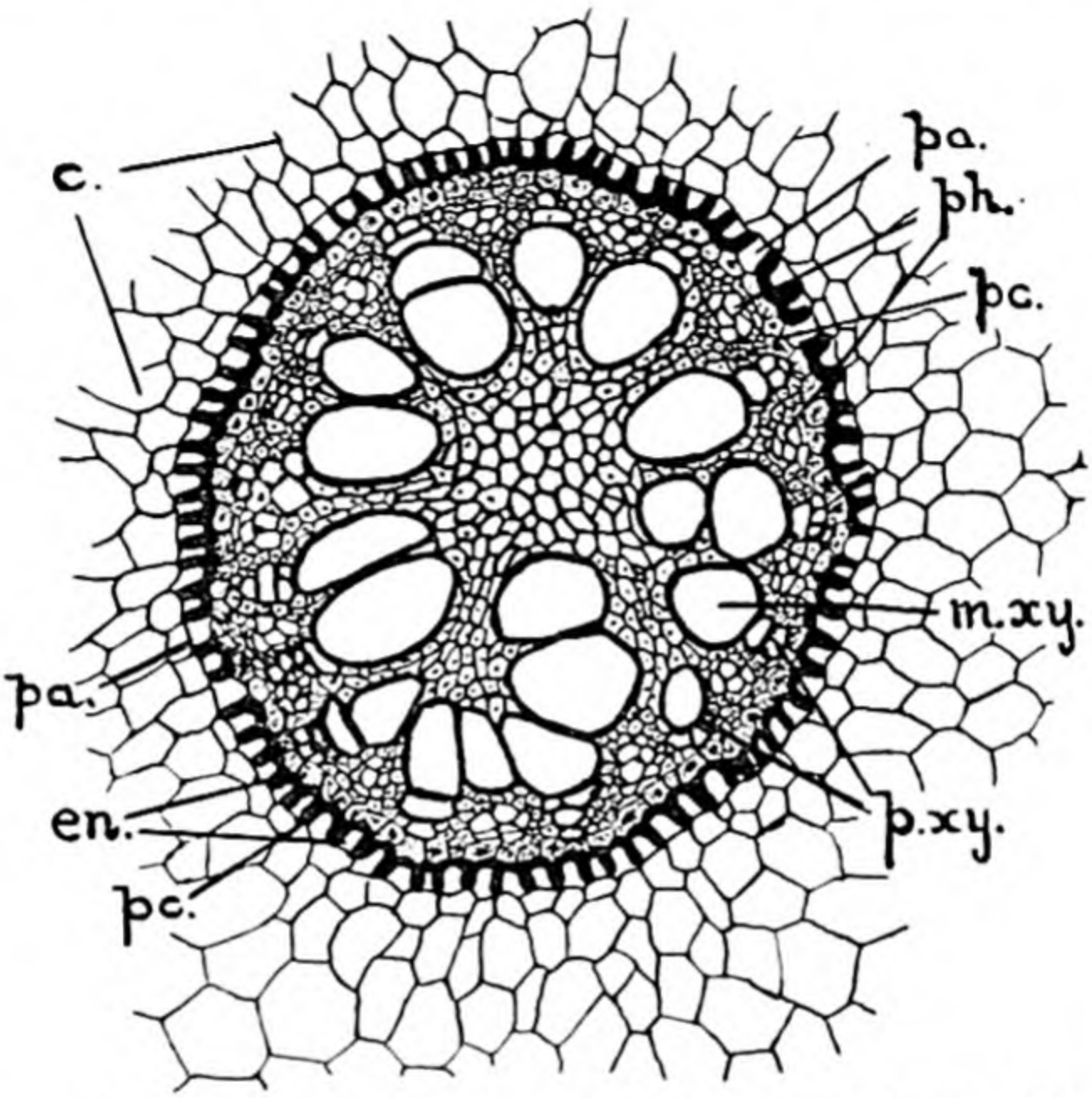


FIG. 201 – Transverse section of the central part of the root of *Iris*. (From 'Plant Form and Function', by F. E. Fritsch and E. J. Salisbury. Bell.)
c., cortex; *en.*, endodermis; *m.xy.*, metaxylem; *pa.*, passage cells; *pc.*, pericycle; *ph.*, phloem; *p.xy.*, protoxylem.

of the stele pith is usually present, affording a ready means of distinction from dicotyledonous roots.

Growing Point

Unlike that of the stem, the apex of the root is covered by a root cap. Beneath this lies a cluster of **initial cells**, from which are eventually derived all the tissues of the mature root. It should be noted in passing that Hanstein described for the root much the same arrangement of layers, or *histogens*, as that already alluded to for the stem (page 246). Again this must be regarded as valuable only as an observational picture, rather than as an expression of the facts of development. The initial meristem consists of several layers of cells, just beneath the root cap. The cells are small closely packed and without vacuoles: they divide continuously. A special layer of this meristem, termed the **calyptrogen**, is

normally responsible for the origin of the root cap. But in most Dicotyledons this calyptrogen is itself derived from the outermost layer of the initial meristem, termed the **protoderm**. In other words, in the calyptrogen itself root cap formation has already been initiated.

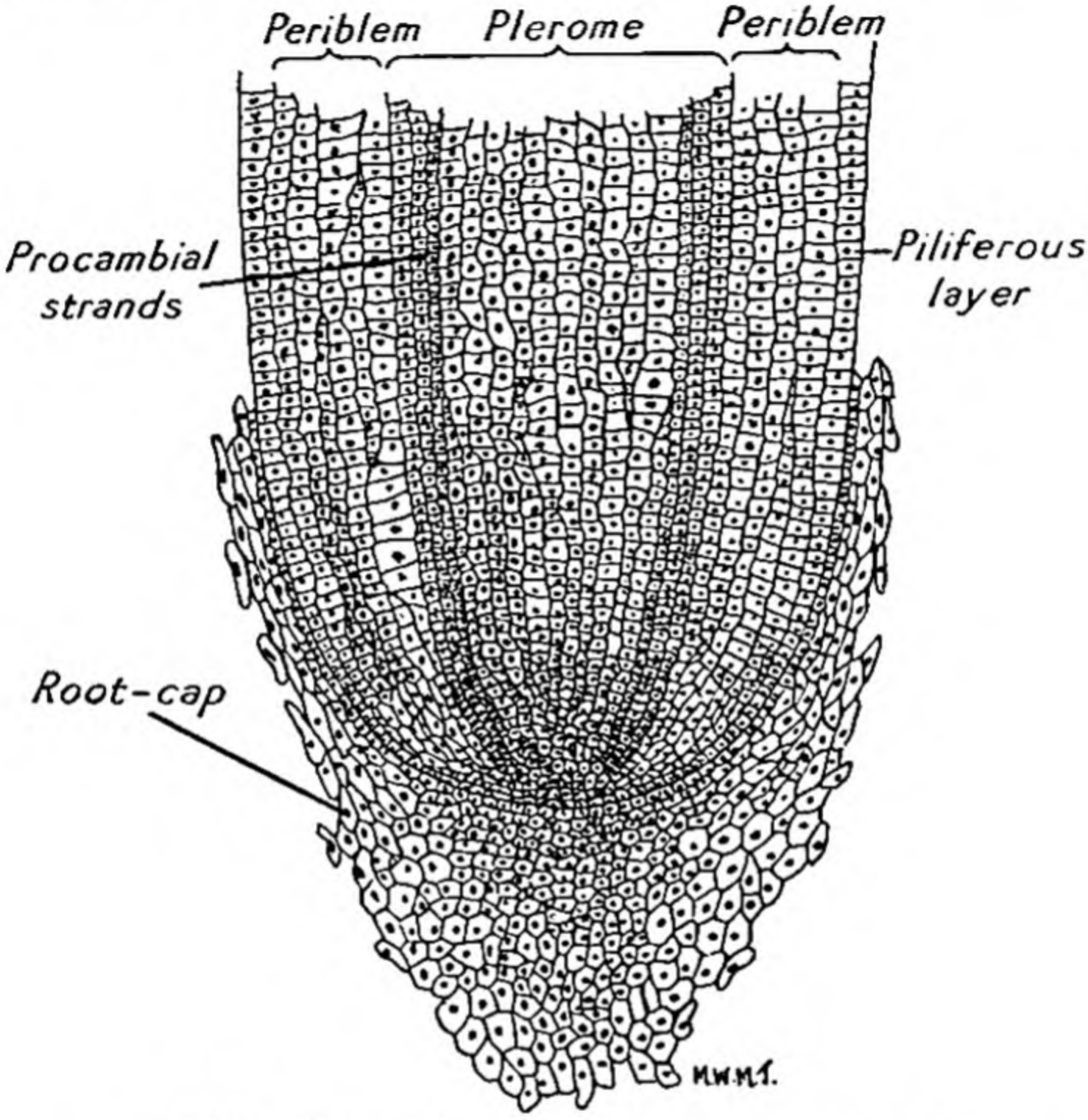


FIG. 202 – *Zea mais*. Longitudinal section of the root-tip.

The first event in the further development of the initial cells in the root itself (as distinct from the cap) is rapid vacuolation, which commences about 3 mm. behind the apex and is confined to the next 2 mm. The increase in size due to this vacuolation is almost exclusively in a longitudinal direction.

Next behind the elongating region the **piliferous layer** (page 290) develops from the protoderm. Each hair arises by the lateral extension of a single cell and thus contributes to the absorptive capacity of this region by increasing the surface area in contact with water. Since these hairs arise from cells behind the elongating region they are not torn off as a result of increase in length of the root. Ultimately the root hairs and their associated cells break away, so that the outermost layer of

the root is really the limiting layer of the cortex; it is called the **exodermis.**

Within the piliferous layer the cortex develops, the rounded cells of which it is composed being arranged radially and enclosing air spaces. The innermost layer of the cortex is the **endodermis,** the cells of which soon become distinguishable by the development, around each cell, of a **Casparian band,** composed of ligno-suberin and found in the radial and horizontal walls. This band binds together the endodermal cells and is impervious to the passage of water. Especially in Monocotyledons, the cells of the endodermis become further modified by the deposition of lignified cellulose over the inner surfaces of their walls. A few, however, remain unthickened, allowing the movement of water through the otherwise impervious layer: these are **passage cells.**

Within the endodermis the **pericycle** appears as a single layer of thin-walled cells which retain their powers of division. They are, in fact, responsible for the origin of branch roots, as indicated below. At the time of differentiation of the pericycle the whole of the centre cylinder of the root is to be regarded as procambium, from which arise the xylem and phloem elements, the latter appearing first (see Fig. 203). Bearing in mind the final appearance of the young root, a careful study of Fig. 203 will indicate the way in which their differentiation is effected. It should be noted that, in most Monocotyledons and some Dicotyledons (e.g., *Ranunculus repens* – page 291), the metaxylem, which develops centrally, is formed from relatively large meristematic cells, though lignification does not occur until all the outer xylem cells are completely mature. As in the stem (page 244) the distinction between proto- and meta-xylem is really one of precedence of differentiation, rather than of structural discrimination, though in general the cells of the latter are larger than those of the former, simply because they are not formed until cell enlargement by vacuolation is complete. There is no possible structural distinction between proto- and meta-phloem.

Branching

Lateral branches normally arise from the cells of the pericycle. Thus their origin is described as **endogenous,** commencing deep in the tissues of the main root, in sharp contrast with the exogenous origin of the lateral members of a stem. At first the cells of the pericycle divide both tangentially and radially, thus forming a peg-like structure, which, as it extends outwards, pushes in front of it a small portion of the endodermis. The cortical cells in its path are disrupted and some differentiation of the branch rudiment becomes apparent, following a similar pattern to that occurring in the main axis. First a root cap appears, and this is followed by the acropetal differentiation of the vascular elements, this process commencing at a point where contact with the corresponding tissues of the main root is established. After emergence the endodermal cap is cast off.

The endogenous origin of branch roots is presumably of protective significance, since there are no leaves to cover the delicate growing point, as in the stem. By delaying the time of emergence of the branch it is

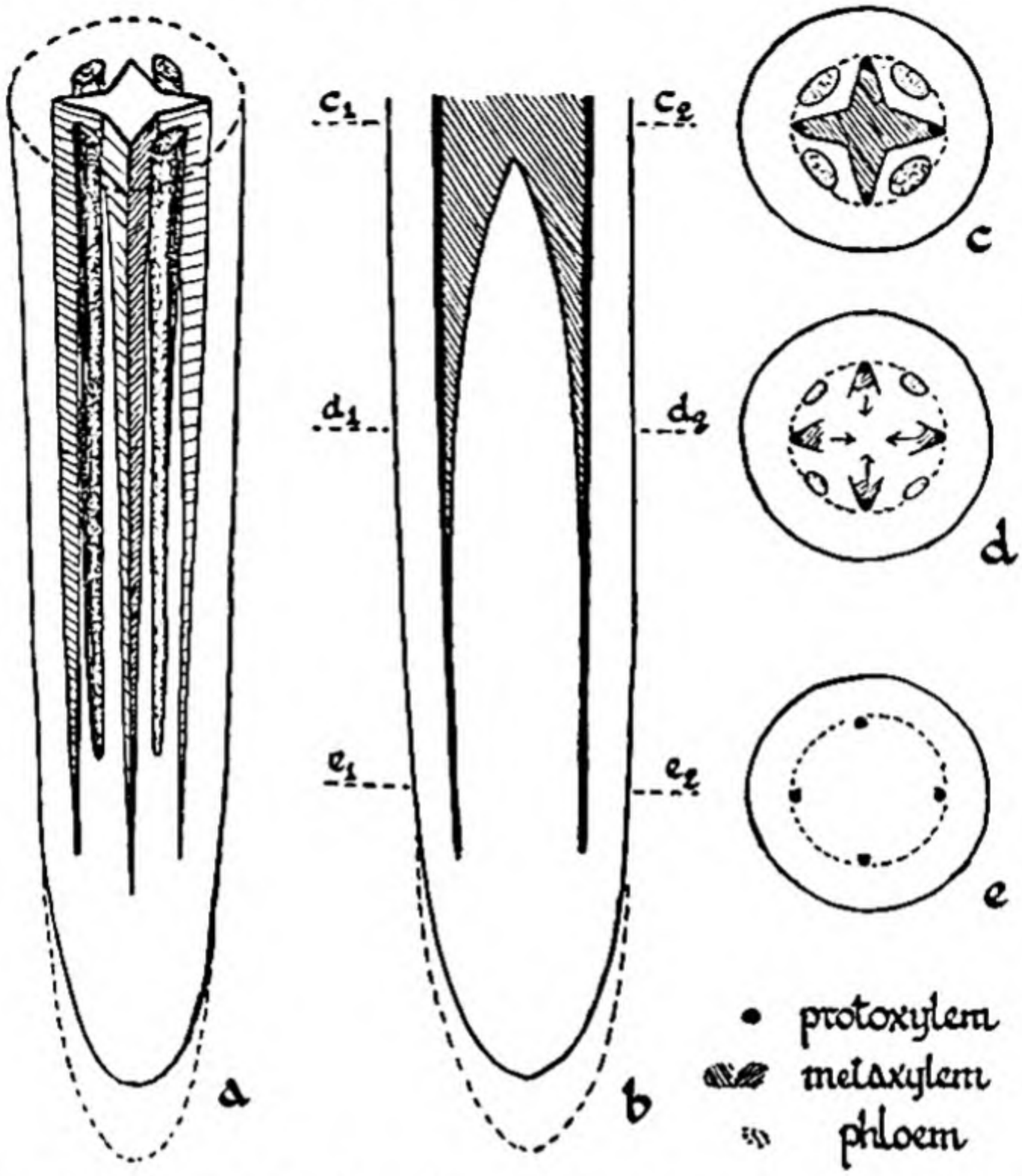


FIG. 203 – Diagrams to show differentiation of vascular tissue behind the root apex. *a.*, showing phloem (dotted) and xylem (shaded) as they would appear if other tissues were transparent; *b.*, longitudinal section of the same; *c.*, *d.* and *e.*, transverse sections taken at the levels c_1, c_2, d_1, d_2, e_1, e_2, respectively in Fig. *b.* (From 'Plant Biology', by H. Godwin. Cambridge University Press.)

virtually certain that it will, by then, have formed its own protective cap. This same delay also prevents interference either with the growth of the main root or with the physiologically important root hair region.

Secondary Thickening

This is effected in a manner closely analogous to that already described for the stem (page 248). Cambium is formed by de-differentiation of parenchyma cells and appears first in the form of a number of arcs, one

on the inner side of each phloem bundle. From these arcs are proliferated new xylem cells on the inner side and new phloem cells on the outer. Thus opposite each arm of the primary xylem is left a space occupied by parenchyma only, as seen in Fig. 204, II. These spaces are the **primary**

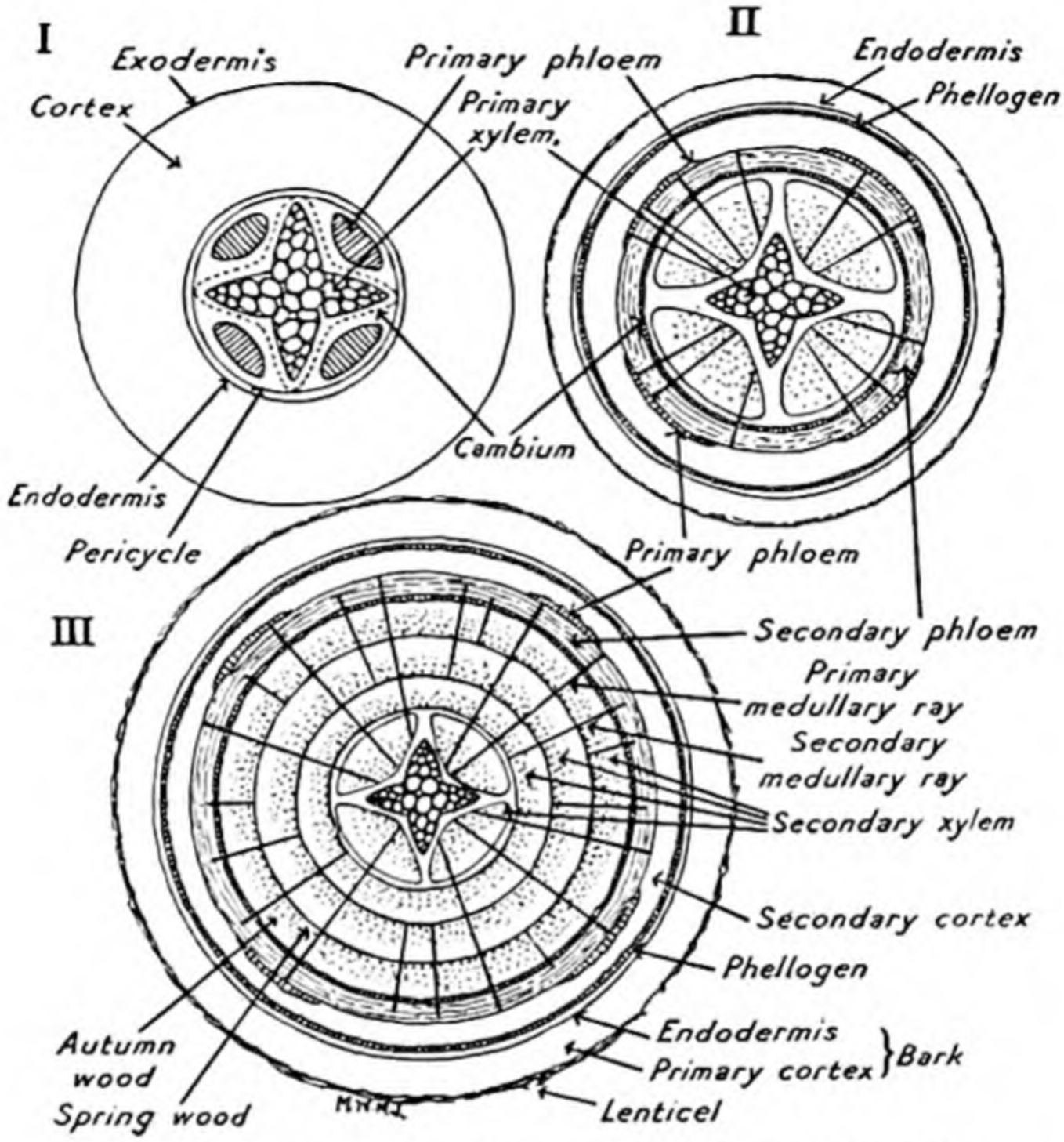


FIG. 204 – Diagrams to illustrate the course of secondary thickening in the root of a Dicotyledon.

medullary rays. When these cambial arcs are pushed out as far as the pericycle this latter converts them into a continuous layer, which, although somewhat undulating at first, soon becomes circular. From this point onwards it produces a large amount of secondary xylem on its inner side and much less secondary phloem on its outer. Smaller (secondary) medullary rays are formed at intervals, as in the stem, whilst **annual rings** become apparent in the secondary xylem. Soon after the inception of secondary thickening the pericycle becomes a **phellogen**, or *cork cambium*. By tangential divisions this gives rise to a number of concentric layers of cork cells, constituting the **phellem**. As in the stem, the phellogen and all tissues external to it form the **periderm**, or *bark*, interrupted at intervals by **lenticels**, again as in the stem.

Hypocotyl

The vascular elements – xylem and phloem – of the root are continuous with those of the stem, and yet their arrangement in the two parts is so different. It is essential, therefore, to investigate their course in the transitional region. This region is known as the **hypocotyl**, and is the part

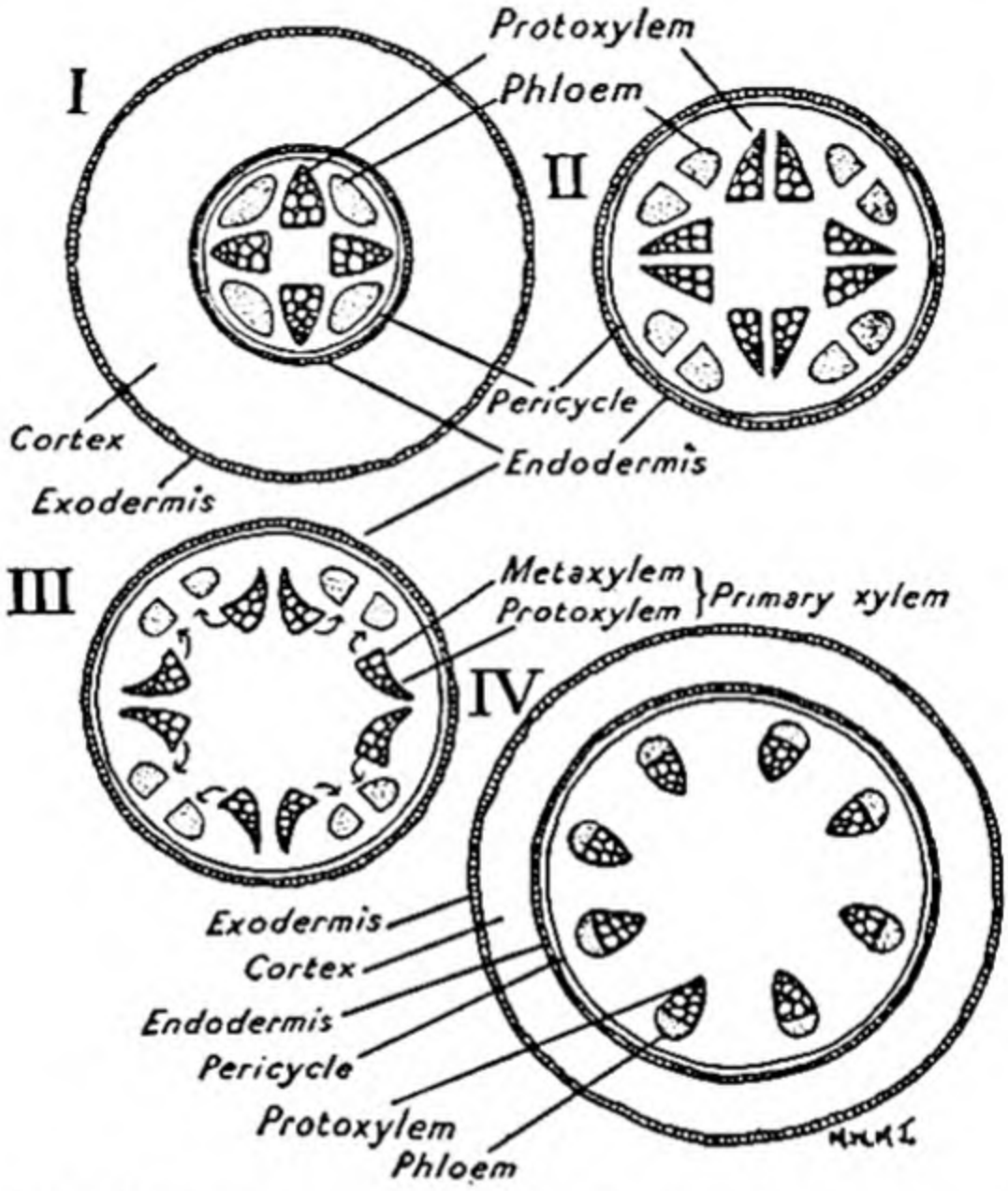


FIG. 205 – Diagrams to represent the structure in transverse section of various regions of the hypocotyl, passing from root to stem.

of the stem immediately below the cotyledons; it can be readily obtained from a young seedling. A series of sections through the hypocotyl demonstrates the following events in the course of the xylem and phloem through that region. Passing upwards from root to stem each strand of xylem and phloem becomes divided radially into two halves. These move apart in such a way that there are twice as many collateral bundles in the stem as there were strands of xylem or phloem in the root. As this alteration in position is taking place the xylem becomes rotated about its vertical axis, so that the protoxylem, outside in the root, occupies the extreme inside position in a vascular bundle of the stem. These changes are represented diagrammatically in Fig. 205.

PRACTICAL WORK

Examine and sketch a tap root (carrot, parsnip, beetroot, etc.) and a fibrous root – e.g. garden nasturtium. Examine and sketch a *Dahlia* root to show tubercles.

Germinate a pea or bean and examine the entire root-tip under low power. Note the root-cap and root-hairs. Sketch.

Cut longitudinal sections of the root-tip to investigate the structure of the growing point. Draw carefully.

Examine a number of available plants to discover the relationship between leaf-arrangement and the type of root.

Split a leaf of *Begonia* and lay on moist soil. Adventitious roots may be formed.

Cut and examine transverse sections of a young root of a Dicotyledon (e.g. *Helianthus*) and a Monocotyledon (e.g. *Iris*). Stain the thin sections as described for the stem (page 252). Make a careful drawing.

Cut and examine sections of a root of *Helianthus* some distance behind the root-hair region. The early stages of growth in thickness may be observed.

Examine and draw prepared sections of a thickened root of *Helianthus*. Concentrate on the way in which you would distinguish it from a stem equally thickened.

Investigate the structure of the transition region between root and stem by cutting a series of sections through the hypocotyl of a bean seedling. Draw representative stages.

PART III

Cellular Structure of Organisms

So far the anatomy of animals and plants has been considered primarily in respect of gross structure of parts. But the majority of organisms are divided up into cells, and these may be regarded as the ultimate unit of such subdivision. In the Protozoa and non-cellular Algae the anatomy can obviously be considered in no more detail than has already been done in Chapters 1 and 9. But in the remainder it is possible to study the structure of the various types of cell into which the organism is divided. This constitutes **histology**, involving the discovery of the broad features of construction of individual cells. This is attempted by the description first of all of a hypothetical, typical cell, somewhat different in animals and plants. Since all cells are developed from pre-existing cells by division, the mechanism of this process is then considered. This involves a knowledge of the minute structure of the nucleus. Such a detailed study of cellular structure constitutes **cytology**. With a knowledge of the structure of a typical cell the modifications required to convert this into the components of various animal and plant tissues are readily appreciated.

In this section the relation of structure to function is repeatedly emphasised. The phenomenon of division of labour within the body of the animal or plant is discussed, after which it is considered to what degree the application of this principle may be extended to animal and plant communities.

CHAPTER 18

The Cell and its Contents

So far the study of the structure of animals and plants has resolved itself into a consideration of their gross anatomy, wherein organs have been described and their material connexion with other parts of the organism noted. But it is now necessary to investigate the structure of individual parts of both animals and plants in considerably more detail, attempting to discern something of the way in which each of them is made up.

Organisms such as *Amoeba* and *Chlamydomonas* differ sharply from most other animals and plants respectively in that their bodies are not divided up by partitions, but each consists of one continuous mass of protoplasm, that of *Chlamydomonas* being enclosed within a definite wall. But the vast majority of animals and plants are divided up into very small units, termed **cells**, each of which may to some extent resemble a whole *Amoeba* or *Chlamydomonas* individual. As will be seen in Chapter 20 these cells do not all remain exactly alike, but become specialised, or differentiated, to perform particular functions. The cell may, in fact, be defined as the smallest unit of organisation of matter which, in present conditions, is capable of sustaining all the processes which collectively constitute 'life'. In this definition, emphasis must be placed upon present-day conditions, for there is little doubt that when living matter first came into existence the units were much simpler than the modern cell. As for particles of viruses, there is considerable doubt as to whether these possess the properties of life in their own right. Certainly they multiply, but it must be admitted that this capacity for self-reproduction by virus particles is only ever in evidence when they are contained within a living cell. It may well be that reproduction of the virus particles is dependent upon the division mechanism of the cell containing them. But there are certain fundamental properties possessed by almost all cells, and in order to acquire some idea of these characteristics a hypothetical typical cell will now be described, essentially similar in animals and plants.

Typical Cell

A typical cell consists of a mass of living matter, or **protoplasm**. The normal size varies from 10 to 100μ, such limitations being set by the surface/volume ratio, so important in view of the fact that the cell depends so greatly upon exchanges of materials with its surroundings. Near the centre lies a spherical body, termed the **nucleus**, enclosed by a double

membrane. Contained within the nucleus are one or more large, spherical bodies. These are the **nucleoli** (see also page 310), whose staining properties vary not only between different types of cell but also at successive phases in the life of the same cell. The living matter of which it is composed is termed **nucleoplasm**, distinguishing it from that which comprises the remainder of the cell – termed the **cytoplasm**. Cytoplasm has been shown to possess a very definite architectural structure in three dimensions, and this state of affairs is largely inferred from the process of development from egg to adult. The actual structure is resident in the protein molecules, since they alone possess a sufficient degree of complexity. There are, in fact, three separate protein components, namely, very soluble, dispersed, globular molecules, a set of rather less soluble semi-filamentous molecules, and finally a group of even more insoluble filamentous molecules. In specific parts of the cell and under certain conditions these filamentous molecules join together endwise to present an orderly 'crystalline' array, and especially is this so at cell surfaces

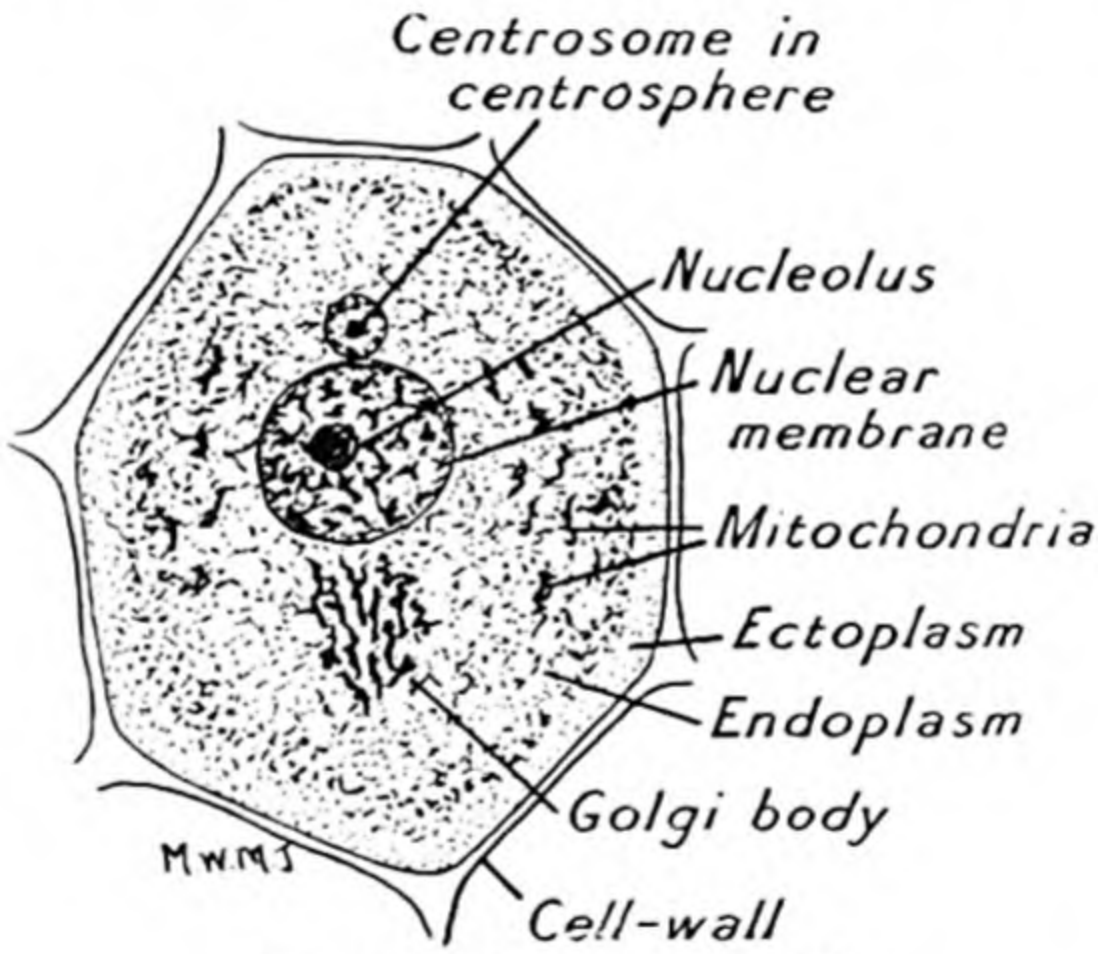


FIG. 206 – Typical animal cell.

and in contractile cytoplasm. Thus in cilia, flagella and muscle fibres these conjoined protein threads lie along the main axis during periods of inactivity, but during contraction they exhibit partial disintegration. Furthermore, cleavage during cell division is likewise the result of similar superficial cytoplasmic contraction, rather than of change in the surface tension of the cell membrane. The cytoplasm itself is not of uniform composition, and may frequently be seen more or less clearly divided into an inner, granular **endoplasm** and a peripheral, clear **ectoplasm**. This condition has already been noted in *Amoeba* and *Paramecium*. In plant cells the arrangement is typically different from this, for the cytoplasm is

confined to two regions, one lining the cell-wall, and one surrounding the nucleus. The remainder of the cell is filled with a clear and much less viscous **cell-sap**, constituting the vacuole, traversed by delicate cytoplasmic threads. Alternatively, the nucleus may lie embedded in the cytoplasm lining the cell-wall, in which case the whole cavity of the cell is occupied by the cell-sap. In the cells of animals and of some primitive plants there is to be observed, embedded in the endoplasm near the nucleus, a small rounded body, termed the **centrosome.** Within it is contained a deeply-stained granule, termed the **centriole**. This takes the form of a barrel-shaped cylinder, the walls of which are composed of nine parallel rodlets, held together by two girdles, each consisting of nine macromolecules, joined to the rodlets by threads. The centriole is often immediately surrounded by a clear region of cytoplasm, known as the **archoplasm**. The centrosome has never been observed in the cells of higher plants. There are also present in the endoplasm some twenty different kinds of suspended particle. Of these, the mitochondria, lysosomes and microsomes and Golgi apparatus are the most important. **Mitochondria** are elongated bodies of length about 500 millimicrons. Each is surrounded by a double membrane and contains tubular or paired lamellae, termed *cristae*, which themselves bear densely accumulated, minute particles, about 10 millimicrons ($\mu\mu$) in diameter. The **lysosomes** are smaller and each appears to be sac-like in structure, containing a homogeneous fluid. The **microsomes** are even smaller, having a diameter of about 100 $\mu\mu$. They are vesicular or tubular, bearing, on their outer surfaces, particles of the same size as those present on the mitochondria. The **Golgi apparatus** (or body) is compact and consists of a series of parallel membranes. These are very thin and, in internal structure, not unlike the mitochondria. Indeed it has been suggested that mitochondria are actually derived from the Golgi apparatus. Other particles present in the cytoplasm include **Nissl granules** (page 335), **myofibrillae** (page 333), basal granules of cilia or flagella, fat droplets and granules of metabolic by-products. The function of the Golgi material has been largely investigated by Duthie, working on the pancreas of mice. He has reached the conclusion that intra-cellular secretory products originate under the influence of mitochondria and are subsequently modified chemically by the Golgi material, which is widely dispersed through the cell during periods of secretory activity. The material may act as a condensation membrane, serving to concentrate the products, may itself actually synthesise or may produce intracellular enzymes. Furthermore, it is probable that much of the fatty yolk contained in eggs is produced by the Golgi material. Myofibrillae (page 333) constitute a special component of the cytoplasm, as do the basal granules of cilia and flagella. Amongst the non-living inclusions are Nissl granules (page 335), fat droplets and granules of metabolic by-products.

The mitochondria, as noted above, are important for their secretory

activity. In the Protozoa they probably provide the source of digestive enzymes and it is believed that they play some part in the physiological processes of spermatozoa and other non-secretory cells. In this connexion their possible influence on the respiratory process cannot be ruled out. Similar functions have been attributed to the microsome.

Mitochondria have been displayed in all plant groups except the Bacteria and blue-green Algae. A close comparison may be drawn between some virus particles (e.g. tobacco mosaic) and mitochondria. In the present state of our knowledge no definite pronouncement can be made regarding the existence of Golgi material in plants. It is of interest to note that one authority believes that the plastids of plants correspond to the Golgi material of animals.

The outer limit of the cytoplasmic component of the cell is marked by the presence of a **plasma membrane,** or **plasmalemma,** which must not be confused with the cellulose wall of plant cells or the skeletal carbohydrate or protein wall of animal cells, for these have a purely mechanical function. The true plasma membrane is composed of a double layer of elongated phospholipid molecules, the greater part of the length of each of which exhibits lipid properties, the terminal portion consisting of a polar group. This double layer, 70 to 100 Å thick (1Å = 10^{-8} cm.), is supported inside and outside by a meshwork of filamentous protein molecules (page 302). The plasma membrane serves to establish and maintain the differential between the contents of the cell and those of the environment. For example, in the cells of aquatic organisms there always exists a greater concentration of potassium relative to sodium ions than in pond or sea-water. It readily allows the passage of small, uncharged molecules, but of ions only very slowly, since much adsorption occurs. Relatively large molecules are transmitted comparatively rapidly in many cases, presumably by an elaborate secretory process, which may operate against the concentration gradient, as in the case of the resorption of glucose from the kidney tubules into the blood.

Little can be added to the above in respect of the typical animal cell, but the corresponding structure in plants may be profitably considered in more detail.

The Plant Cell

This may be studied in respect of (*a*) the cell wall, and (*b*) the cell-content.

(A) THE CELL-WALL. The wall of a typical plant cell rarely consists of anything like pure **cellulose**. An important exception to this is afforded by the cell-wall of cotton hairs. Cellulose, a polysaccharide, consists of long, thin threads, or *microfibrils*, composed of chains of molecules; their width is approximately twice their thickness. These microfibrils act as a core, within which are parallel chains of β–D–glucose residues, whilst surrounding the core is a cortex, consisting of chains of sugar residues

other than glucose. These are commonly referred to collectively as **hemi-celluloses** and are mainly branched polymers of xylose, mannose and related sugars. This cortex prevents the packing necessary to impart true crystallinity to the microfibrils, which are best described as para-crystalline. This term signifies a condition, often applicable to long, chain-like molecular groups, including such substances as silk, nylon and stretched rubber, where there is no sustained regularity of packing, but over limited portions there is an orderly pattern in the form of true linear array. As well as cellulose, some cell-walls contain various compounds of pectic acid, common amongst which is the calcium salt, **calcium pectate** (see page 376). Pectic acid itself is a compound formed between certain sugars and a somewhat similar compound, galacturonic acid. The middle lamella[1] – the first layer of the wall formed after nuclear division – consists entirely of pectic substances.

This simple wall may become variously modified. It may become thickened by the addition of fresh cellulose-pectic substances around its lining, either at certain points or uniformly throughout. The walls may become impregnated by a substance, known as **lignin**, of importance on account of the fact that it results in stiffening the walls, resulting, however, in considerable loss of permeability. On the other hand, they may become impregnated with **suberin**, forming typical cork. The walls of these cells are completely waterproof. The formation of **cutin** by the cells of the epidermis of plants is peculiar in that this substance is deposited outside the cell, the continuous layer thus formed constituting the cuticle. This also is impermeable to water. Finally the cell-walls may absorb large quantities of water and thus give rise to **mucilage** by the formation of a loose sol (page 307). In this way the characteristic mucilage of *Fucus* is produced. The various parts of the plant where such modifications occur are detailed in Chapter 20. In conclusion, it should be noted that the walls of the hyphae of Fungi contain a core, not of cellulose, but of chitin. The two compounds are basically similar. Such differences in chemical nature as exist may be related to peculiarities of the nutritional habits of Fungi.

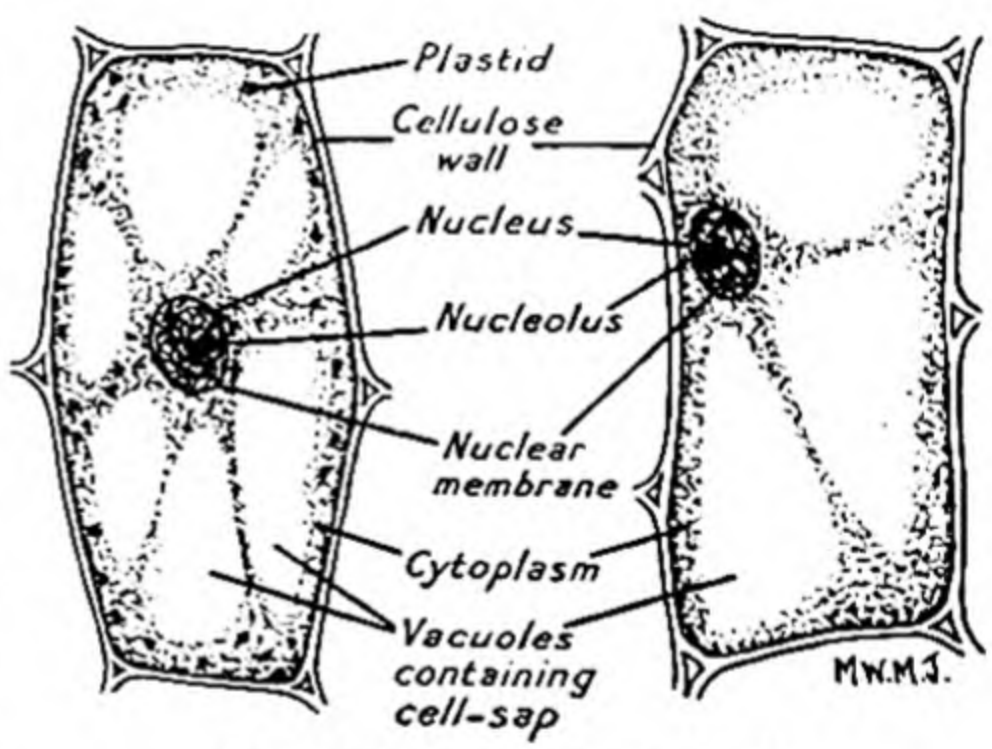


FIG. 207 – Typical plant cells.

(B) THE CELL-CONTENT. Immediately lining the cell-wall and sur-

1. See also page 316.

rounding the nucleus the cytoplasm remains clear, and these two regions constitute the **plasma membranes** (page 304). The remainder of the cytoplasm is granular, and amongst its more important inclusions may be noted certain small, rounded bodies, known as **plastids**. The majority of these bodies, occurring in the stem and leaves are green in colour, owing to the possession of the characteristic plant pigment, chlorophyll, and are consequently termed **chloroplasts**. Though normally biconvex in shape they may assume other forms. Thus in each cell of a filament of *Spirogyra* the single chloroplast is in the nature of a spiral band, though still contained within the cytoplasm lining the cell-wall. In parts of the plant not exposed to light the plastids remain colourless and are called **leucoplasts**. They may be found, for example, on the underground shoots of the potato plant. The essential similarity between chloroplasts and leucoplasts may be shown by the fact that the latter develop chlorophyll when exposed to light, and thus become indistinguishable from chloroplasts. In some Algae there may also be distinguished small, colourless patches of protein material. These are **pyrenoids**. They occur embedded within the chloroplasts, and are associated with the deposition of starch. Contained within the plastids are found starch-grains, the structure of which is described on page 406.

As well as the **protoplast** (cytoplasm *plus* nucleus) the cell-sap is an extremely important feature of plant cells. It consists essentially of an aqueous solution of certain sugars and mineral salts, and in consequence is able to exert an appreciable osmotic pressure[1], as a result of which an important experimental observation may be made. A thin section of beetroot is washed free from superfluous colouring matter and then placed on a glass slide, being then mounted in a 12% solution of glucose. As a result it is observed that the protoplasmic contents of the cell become withdrawn from the wall, owing to the fact that a certain quantity of the solvent (water) of the cell-sap has been withdrawn. This phenomenon is known as **plasmolysis**, and depends upon the fact that the 12% solution of glucose exerts a greater osmotic pressure than does the cell-sap. If the plasmolysed section be now mounted in distilled water it is found that the protoplasmic layer recovers its position of a lining to the cell-wall, since water has this time entered the cell-sap from outside, where there is no osmotic pressure generated. In normal conditions it is presumably the cell-sap which keeps the protoplasmic layer fully distended so that it lines the cell-wall.

By an application of a knowledge of plasmolysis it is possible to calculate to an approximate degree the osmotic concentration of the contents of the cell-sap. Thus sections of beetroot, prepared as indicated above, are mounted in a series of solutions of glucose ranging from 12·0%

1. If the student is not already conversant with the phenomenon of osmosis he is advised to read pages 376 to 378 before proceeding further with the present chapter.

downwards, each differing from the predecessor by 0·5%. Knowing that a 12% solution gives an osmotic pressure of 14·93 atmospheres at 0° C., it is possible to calculate the osmotic pressure of the cells of the plant under consideration when it is discovered by observation what strength of solution just fails to cause plasmolysis. Such a solution is said to be **isotonic** with the cell-sap. For some plants a 12% solution may not be sufficiently concentrated to cause plasmolysis, so that for the starting-point of an experimental determination of the osmotic pressure of its cells a more concentrated solution must needs be employed. The osmotic pressure of some desert plants, for example, may reach as much as 150 atmospheres.

It is possible for sea-water to be employed for experiments on plasmolysis. It might be imagined that a solution of any single salt – e.g., sodium chloride – of such strength that it would generate the same osmotic pressure as the corresponding solution of sea-water would do equally well. But this is not the case. Some ions when occurring alone exert a toxic (poisonous) influence on the cytoplasmic lining, whose permeability is thus modified, allowing the passage of more water than would otherwise be permitted. But certain mixtures of ions in solution are not harmful in this way to the cytoplasm, and such mixtures are referred to as *balanced* solutions. The ions are said to *antagonise* each other's deleterious influences on the cytoplasm.

Physical Nature of Protoplasm

The state in which the various chemical constituents occur in the protoplast is important, since almost every gradation from a true solution to a suspension is encountered. The proteins are present in **colloidal** state. There is, in fact, no hard and fast distinction between crystalloids and colloids, but something of an analysis of the problem is essential here. Colloidal solutions (*sols*) appear to be optically homogeneous when viewed with the naked eye or through a microscope. That this is not strictly the case can be demonstrated by means of the ultramicroscope. Here the microscope is placed at right angles to the beam of light illuminating the solution. Separate particles then become visible as a result of the scattering of rays of light impinging upon them (the Tyndall effect). Colloidal solutions are thus two-phase systems, consisting of a *disperse phase* (the particles) and a *continuous phase* (or *dispersion medium*), corresponding to the solvent of a true solution. A somewhat arbitrary distinction between a true solution and a colloidal solution is based upon the size of the particles. Colloidal particles vary in size from 5$\mu\mu$ (the lowest limit detectable by the ultramicroscope) and 150$\mu\mu$ (the lowest limit of visibility with an ordinary microscope).

Colloidal solutions are further divisible into two categories – *suspensoids* (where the disperse phase is a solid) and *emulsoids* (where the disperse phase is a liquid). One notable property of colloidal particles is

their Brownian movement. Most of the particles, viewed by means of the ultramicroscope, are in a state of oscillation, but occasionally one darts off in a given direction for a considerable distance. This is believed to be due to occasional collision between the colloidal particles and molecules of the dispersion medium. If the particles are not relatively too large they acquire a considerable velocity as a result of the impact.

Emulsoids, unlike suspensoids, are capable of undergoing gelation or coagulation. If an emulsoid sol is concentrated by evaporation and allowed to cool slowly, it gradually stiffens to become at least semi-solid. This is *gelation. Coagulation* is similar in effect but occurs suddenly and at a definite temperature (e.g. the coagulation of egg-white on boiling). The final result in either case is a *gel.* This is still a two-phase system, with a honeycomb structure formed of a highly concentrated and viscous phase, enclosing more dilute and labile solution in the 'cells'.

Colloids and crystalloids may be separated by *dialysis*. This depends upon the use of a dialytic membrane, such as parchment, on to which the mixed 'solution' is poured. Solvent and crystalloid solute alone pass through the membrane.

Protoplasm in the living state normally exhibits no optical structure – e.g., no network is visible. But in some forms it appears vacuolated, as exemplified by Heliozoa (Protozoa belonging to the same class as *Amoeba*). But even here the vacuolation is much less marked in marine forms, so that it may appear as a result of osmotic activities and not be an essential structural feature. Echinoid eggs appear to consist of an emulsion, containing granules of two sizes in a fluid matrix. These granules can, however, be largely segregated by means of the centrifuge without impairing the properties of the protoplasm. The granules are confined to the periphery, whilst in the clear (hyaline) mass within, the mitotic spindle appears, showing that the normal properties of cytoplasm are still retained. Further, if an egg treated in such a manner be fertilised, normal development occurs. These experiments demonstrate the essential fluidity of protoplasm. If protoplasm is a colloid and the continuous phase is water, then protoplasm and water should be miscible. This is often not the case, though miscibility with certain aqueous solutions is almost always observed. The best conception of protoplasm is as a colloidal emulsion, the continuous phase of which consists of an aqueous solution of various crystalloids and electrolytes. It is certain that the disperse phase is very sensitive to changes in the continuous phase. With protoplasm existing in such a state it is apparent that the continuous phase will possess an enormous internal surface. It is believed that this results in the attraction of foreign substances by electrical forces, and that in this condition many reactions occur within the plant. This phenomenon is termed **adsorption**, and is allied to the condensation of gases by some substances, notably carbon, which function is also attributed to the very great internal surface of the condensation medium.

Mineral salts and sugars, on the other hand, occur in the cell-sap as true solutions, and they are distinguished from colloids by the name **crystalloids.**

Coenocytes

Though the various cells of a living organism are each normally clearly defined by means of a cell-wall, there are exceptions to this rule, for occasionally, in both animals and plants, there may be found small masses of cytoplasm, containing several nuclei, but exhibiting no division into separate compartments or cells. Such a mass of protoplasm is termed a **coenocyte.** Though it is essentially non-cellular, it is probable that each nucleus controls the activities of a certain region of cytoplasm, which may thus be said to come within its sphere of influence. Such a nucleus and its surrounding cytoplasm is termed an **energid,** thereby distinguishing it from a true cell, the boundaries of which are clearly defined.

In contrast to coenocytes, each of which is multi-nucleate, there may be mentioned in conclusion the occasional appearance of cells without nuclei. Most important amongst these are the mature red blood-corpuscles of mammals.

PRACTICAL WORK

As well as the experiments on plasmolysis suggested in the text the following is suggested:

(i) Cut a dandelion stem longitudinally into four strips. These at once curve outwards, since the outer layers are in a state of tension. One strip is now placed in distilled water and another in a 2% sea-water. The one in distilled water is observed now to bend more than ever, since the inner (pith) cells absorb this water by osmosis, and thus expand. But the reverse occurs with the strip placed in the sea-water. The pith cells are plasmolysed, resulting in their contraction, so that the strip bends in the reverse direction.

(ii) Examine the hyphae of *Mucor* under oil-immersion. Note that they are coenocytic.

CHAPTER 19

Multiplication of Cells

Almost every organism commences its life as a single cell, in the form of an egg-cell, or ovum, which has been fertilised by a sperm. Fertilisation involves the penetration of an egg by a spermatozoön, which is itself little more than naked nucleus. This nucleus fuses with that of the egg, and the resultant body is known as a zygote, the double nucleus being completely merged into one composite whole. The growth and development of the zygote eventually to form an adult organism is effected by a series of divisions, the component or daughter-cells remaining attached, and not becoming separated as they do, for example, in the process of reproduction in the majority of Protozoa. In this repeated cell-division it is the behaviour of the nucleus which is of primary importance, and hence it is essential that its structure should first be studied in detail.

Nucleus

The nucleus is enclosed by a double **nuclear membrane,** containing within it the **nuclear sap,** or **nucleoplasm,** and colourless threads, known as **chromosomes**, of which much more will be said later. As well as these there may occur within the nucleus bodies known as **nucleoli**. It has been suggested that these latter are essentially cytoplasmic in nature. But this is now known not to be the case, since portions of cytoplasm accidentally included in the nucleus are quite different in appearance from either the nuclear sap or nucleoli. The nuclear membrane itself, during microdissection, can be indented and eventually punctured by pressure. It has recently been suggested that the membrane in life is nothing more than an interface, having the property of semi-permeability. The nucleus is usually spherical, but may be somewhat irregular – e.g. in leucocytes (page 327) – or branched, as in some secretory cells of various insects. In exceptional cells – e.g., the spermatogonia of the grasshopper – the nucleus consists of a number of vesicles, each of which contains a separate chromosome. The description of the nuclear sap as consisting of a network of threads, containing the more fluid sap in its interstices and with granules of chromatin at the nodes, is now regarded as the result of an artefact of cytological method, bearing little or no resemblance to the living structure. During the resting stage (i.e. the period between consecutive divisions) the cell's chromosomes must be regarded as unfixable, but, as will be mentioned again later, this same consideration does not apply to nuclei engaged in the process of division. The chromosomes,

though normally invisible, are believed to retain their identity during the resting state, and this is largely inferred from the fact that their disposition at the end of one division, when they are visible after staining, is identical with that at the commencement of the next. In some cases certain portions of the chromosomes, known as **pro-chromosomes**, persist during the resting stage. A fixed relationship exists for any type of cell between the size of the nucleus and the volume of the cytoplasm. This is known as the karyoplasmic or kern-plasma ratio. According to Hertwig, who introduced the term, this ratio decreases steadily, immediately following cell division. Subsequently the nucleus increases rapidly in size, and eventually the cell divides. Hertwig's theory may be illustrated by the accompanying graph, showing the changes which occur between two successive divisions. Hertwig claimed that conjugation, as occurring, for example, in *Paramecium*, corrected disturbances in the karyoplasmic ratio, whilst Reichenow further stated that there must be a constant ratio maintained between the volume of the nucleus and the surface-area of the cell.

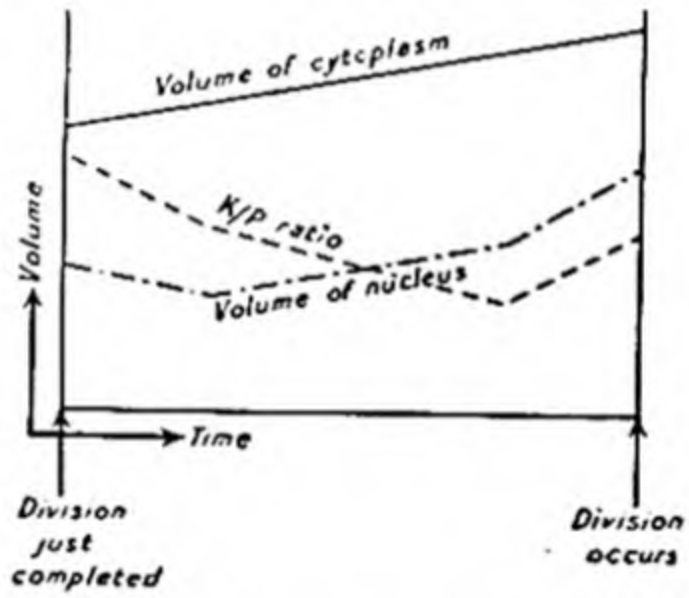


FIG. 208 – Diagram to illustrate Hertwig's Theory.

Cell-division involves two distinct processes. In the first place the fission of the nucleus into two identical halves must occur, followed by an equal (usually) constriction of the cytoplasm. In a few forms it is claimed that the former is effected simply by the elongation of the nucleus to form a dumb-bell-shaped structure, followed by its complete division into two halves. The cytoplasm then becomes constricted so that each mass contains a daughter nucleus. This simple process is termed **amitosis**, and is very much the exception. It has been suggested that, in fact, it does not really occur at all, and that the events described are the result of poor technique and faulty observation. The more usual form of nuclear division is very much more complicated, and is termed **mitosis**. It will now be considered in detail.

Mitosis

For descriptive purposes mitosis is divided into a number of phases,

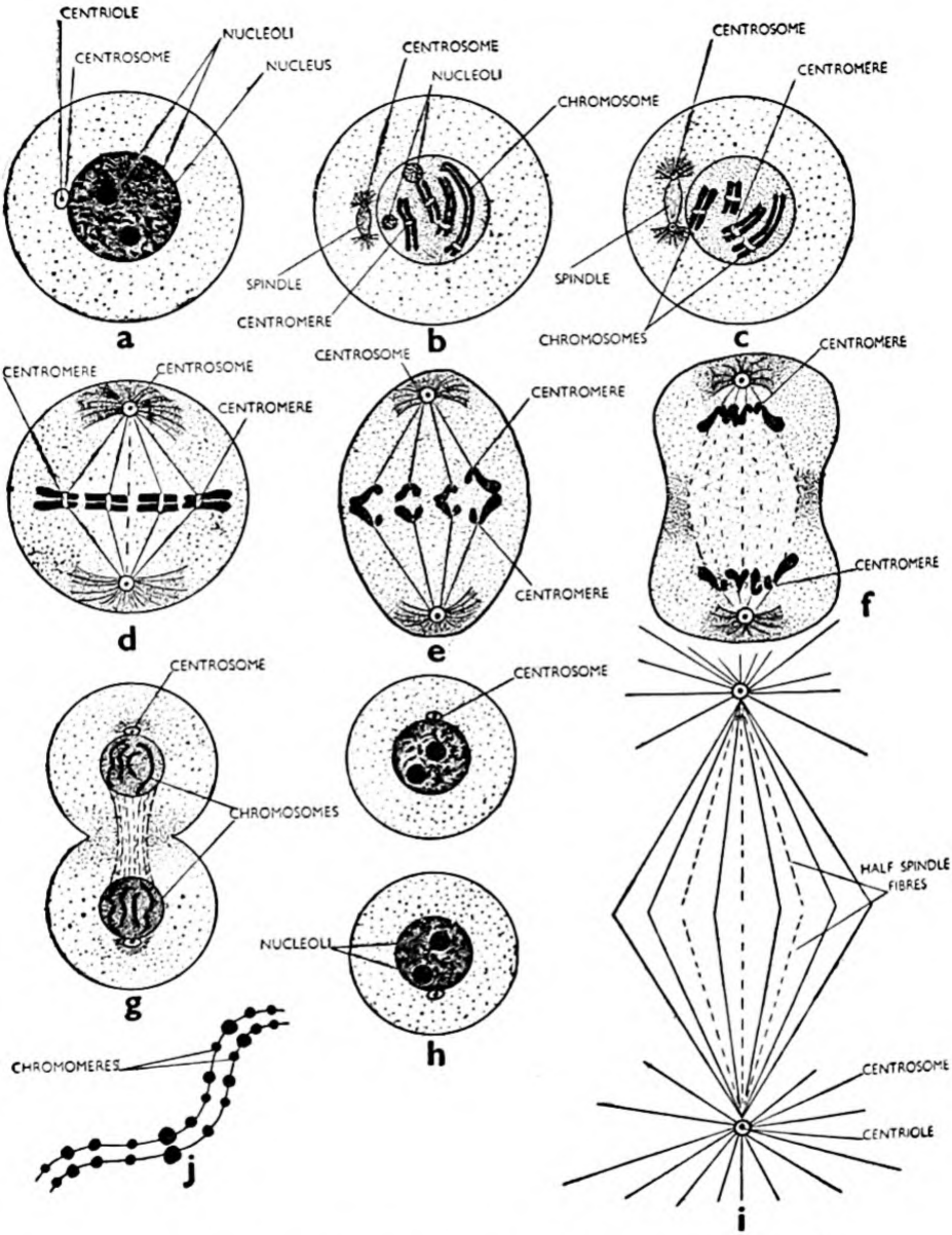


FIG. 209 – Stages in Mitosis. (From *Essentials of General Cytology*, by R. A. R. Gresson. Edinburgh University Press.)

but it must be borne in mind that the process, once started, takes place continuously until completed. The phases are purely arbitrary divisions and have no further significance.

(*a*) *Prophase*. At the outset of mitosis coiled threads appear. These are the **chromosomes**. The fixability of these structures at this and succeeding stages of cell-division is believed to be due not only to the acquisition of nucleic acid (see below) but also to the dehydration which they now undergo, whereas in the resting nucleus they exist in a state of high colloidal hydration. These chromosomes are essentially paired structures, for it is possible to find every chromosome, identifiable by its size and shape, duplicated elsewhere in the nucleus. Not only so, but the number of these bodies is constant throughout a given species of animal or plant. Thus, in the frog, for example, there are twelve pairs, whilst in man there are twenty-three. The two members of a pair of chromosomes are described as **homologous**, whilst the number of pairs present is called the **haploid** number and that of individual chromosomes the **diploid**. For purposes of simplicity only four chromosomes are shown in the accompanying figure, since the remainder behave in an identical manner. The chromosomes at prophase are distinctly longitudinally double, except at the centromere (page 314), the component halves being termed **chromatids**. They now commence to contract longitudinally, and this may continue until they become no more than one-twentieth of their original length. It was formerly held that at this stage the chromosomes coalesced endwise to form a long thread, known as a spireme, but this is now attributed to an artefact of cytological method. The chromosomes are known to be the carriers of heredity factors (Chapter 33), and to have constant composition and properties. It would seem unlikely, therefore, that at every cell-division they should coalesce, only to become separated again almost immediately. Still less likely is it that in the resting cell (i.e., one not engaged in division) they should fragment, as has also been suggested, for this would necessitate not only their reunion to form the same chromosomes as previous to disintegration, but also the recombination of the fragments in precisely the same linear arrangement, for this arrangement is known to be almost invariable (Chapter 33). Much more probable is it that, as pointed out above, each chromosome retains its identity throughout the resting stage, and becomes fixable at the outset of mitosis as a result of dehydration. At prophase the chromosomes do actually appear granular, the separate lobes thus visible being termed **chromomeres**. According to Darlington a chromosome consists of a protein fibre, the **chromonema**, which may acquire from the cytoplasm, at the onset of mitosis, *desoxyribose nucleic acid* (*DNA*), resulting in the formation of chromomeres. As mitosis is completed the same nucleic acid is returned to the cytoplasm. It has been suggested that nucleoli may play some part in this transference of nucleic acid between the chromosomes and the cytoplasm, and this hypothesis is rendered more probable

by the fact that nucleoli appear in the telophase (see below) and disappear in the prophase of mitosis. Though the nucleic acid contained in nucleoli – termed *ribose nucleic acid* (*RNA*) – is slightly different from that of the chromosomes and resembles that of the cytoplasm, it is probable that the two forms are easily interconvertible. It has been established that *DNA* is distributed along the chromosomes in the form of complex molecules and the physical basis of the action of the genes seems to be resident in this molecular arrangement (see page 578). At this stage the two granules of the centriole (page 303) in animals now separate, enclosing between them a spindle-shaped region of cytoplasm. Eventually they come to lie at opposite poles of the nucleus, which is itself completely contained within the **nuclear spindle,** of the same basic structure as the centriole (page 303). The nuclear spindle appears in dividing cells of higher plants without the previous occurrence of a centrosome. That the nuclear spindle is of different nature from the remainder of the cytoplasm is evident from the fact that it can be dissected out.

(*b*) *Metaphase*. Once the nucleus is thus contained within the nuclear spindle its own delicate membrane disappears, whilst the chromosomes become arranged within the spindle in such a way that each chromatid is separately attached, not necessarily at its end, to some point in the equatorial plane of the spindle, the chromatid becoming bearing at this point an **attachment-constriction**, or **centromere**.

(*c*) *Anaphase*. The two chromatids constituting each chromosome now commence to move apart, being separated last at their ends. This process is assisted by the longitudinal extension and transverse contraction of the spindle, though it is probably effected principally by the loss of specific powers of attraction between the chromatids.

(*d*) *Telophase*. The two constituent chromatids of each chromosome now move one to either end (pole) of the nuclear spindle, so that there is now present at each pole the diploid number of chromatids. At this stage the cytoplasm now becomes constricted along a line parallel to the equator of the spindle, which itself becomes thus transversely divided into two halves. Each collection of chromatids thus contained within its own mass of cytoplasm now becomes enclosed in a reformed nuclear membrane, whilst they again become hydrated, and consequently non-fixable. But at the outset of the succeeding cell-division each is found to be longitudinally double, so that this division must have occurred during the intervening resting stage. Once this has occurred they become fully-formed chromosomes.

Summary

Thus the process of mitosis results in the distribution of the same (diploid) number of identical chromosomes to each daughter cell as were present in the parent cell. The significance of this fact will be more fully appreciated when the importance of the chromosomes in the

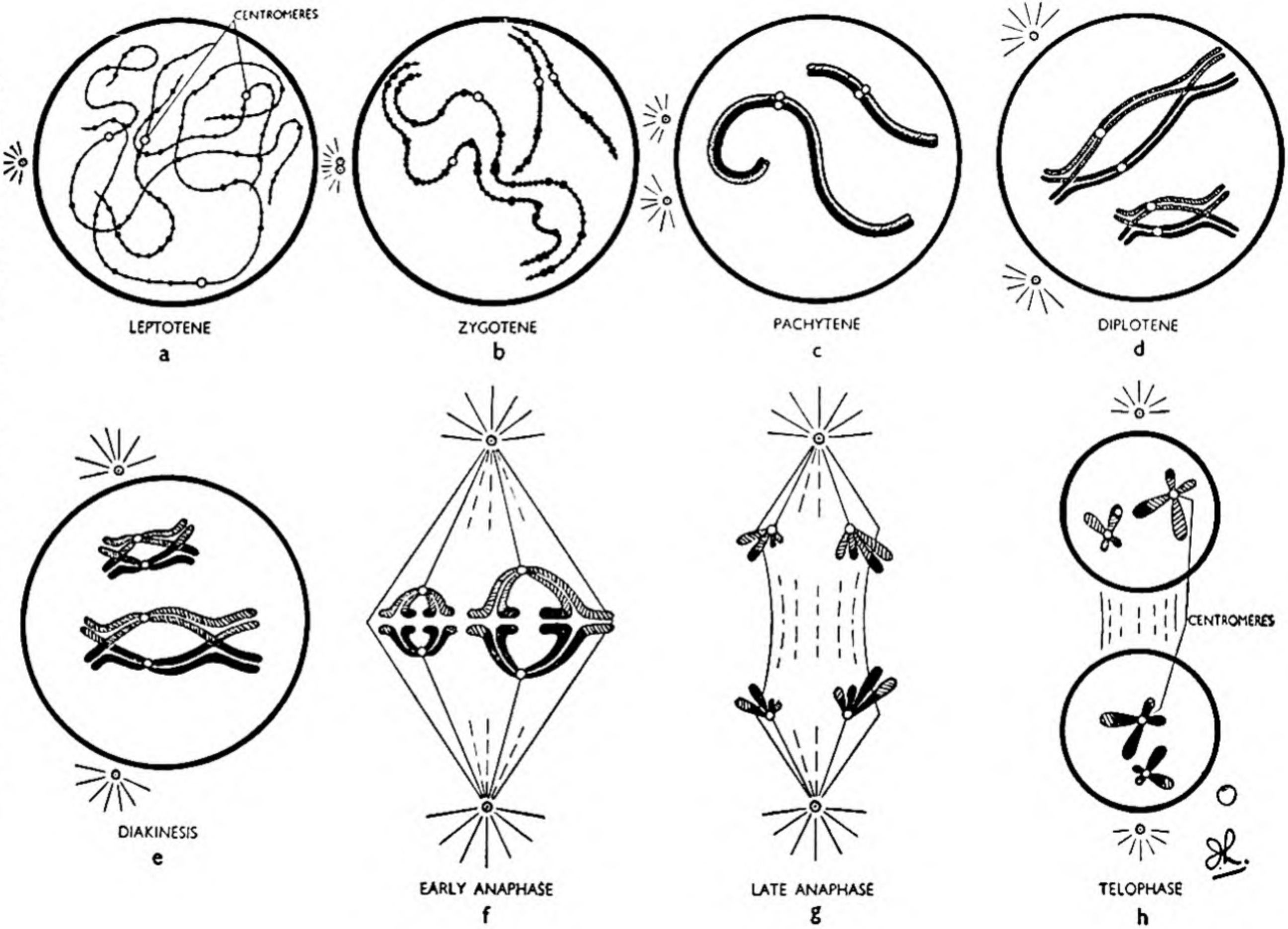


FIG. 210 – Stages in Meiosis. (From *Essentials of General Cytology*, by R. A. R. Gresson. Edinburgh University Press.)

transmission of heredity factors has been discussed (Chapter 33).

The following may serve as a useful summary of the incidents at each phase of the mitosis:

(*a*) *Prophase*. Chromosomes appear, each divided longitudinally into two chromatids and irregularly constricted transversely into chromomeres. The nuclear spindle is formed, enclosing the nucleus.

(*b*) *Metaphase*. The nuclear membrane disappears, whilst the chromatids become attached in the equatorial plane of the spindle.

(*c*) *Anaphase*. Constituent chromatids of each chromosome move to opposite poles of the spindle.

(*d*) *Telophase*. Constriction of the cytoplasm occurs, and changes take place at each pole in the reverse order of that witnessed in the prophase.

There are but few differences in the way in which the process of mitosis is effected in animal and plant cells respectively. In the majority of the cells of at any rate higher plants there is no centrosome present, and the nuclear spindle appears to arise *de novo* from the cytoplasm. Finally, the separation of the two daughter nuclei with the formation of two cells is carried out differently. The method of cytoplasmic constriction described above is typical of animal cells. In plant cells the equatorial region of the spindle begins to show local thickenings, and from these a thin, double wall, known as the **middle lamella**, is eventually formed, extending right across the cell. Subsequently cellulose is deposited on either side of the middle lamella, but the cytoplasm may remain continuous between the cells through minute perforations.

Meiosis

As will be emphasised later, the essential feature of fertilisation is the complete coalescence of twonuclei, normally distinguishable as male and female (Chapter 32). This obviously introduces a new problem in respect of chromosomes, for if both male and female elements contribute a full diploid number there will be a doubling at every such nuclear fusion. But the number of chromosomes is found to remain constant for any given species. It is apparent, therefore, that at some stage of the development of these germ-cells there must be a halving of the chromosome-number to the haploid condition. The peculiar form of nuclear division by means of which this is effected is termed **meiosis**. In animals it occurs during the formation of the actual eggs and spermatozoa themselves, but in plants it is found to take place at a somewhat different stage in the life-history, as pointed out on page 557. But at whatever stage it occurs nuclear behaviour is similar, and it is this which matters at the moment. The following description of this modified process of cell-division is drawn from the pollen mother-cells of *Tulipa* and based on the recent researches of C. D. Darlington. Two divisions are involved in effecting the total reduction, and for convenience each is again arbitrarily subdivided into a number of phases.

(1) First Division

(*a*) *Prophase.* This phase covers a number of changes, and is consequently subdivided into four stages.

(i) *Leptotene.* The chromosomes appear in the form of *single* threads, in contrast with their double nature at the onset of mitosis. Chromomeres, appearing only occasionally in the early prophase of mitosis, are a regular feature of the brief leptotene stage.

(ii) *Zygotene.* Homologous chromosomes (page 313) now come together in pairs and this they do very precisely so that corresponding points of both members are side by side and the entire chromosomes are approximated throughout their length. This is especially apparent when the positions of corresponding chromomeres are studied. Simultaneously the chromosomes shorten and thicken as a result of spiralisation. Each chromosome pair is a bivalent.

(iii) *Pachytene.* Each chromosome now splits longitudinally into two chromatids, while each member of a chromosome pair becomes spirally wound around the other. At this point the forces of attraction which formerly held together the two homologous chromosomes cease to exist. Such attraction now applies to the constituent chromatids of each chromosome.

(iv) *Diplotene.* As a result of the operation of spiralisation and the existence of forces of attraction (between chromatids) and of repulsion (between chromosomes), severe stresses may be set up in the chromatids. In consequence, a chromatid may snap. This relieves the strain in the chromatid involved, but increases it at a corresponding point in the chromatids of the partner chromosome. Thus one of these may break. Immediately the chromatids tend to unwind at this point. The free ends of the chromatids now become united, each with its opposite number, thus forming a **chiasma.** The genetical consequences of this event (which may occur at a number of points along a pair of chromosomes) are discussed in Chapter 33. From the point of view of the mechanics of meiosis it is important in holding together, for the time being, the two members of each pair of homologous chromosomes.

(v) *Diakinesis.* The bivalents shorten and thicken until scarcely recognisable as separate threads.

(*b*) *Metaphase.* A nuclear spindle appears, as in mitosis, and the bivalents are set free by the disintegration of the nuclear membrane. But (and this point should be very carefully noted) there is only one centromere to every associated pair of chromatids of each chromosome. They

become attached to the spindle, again as in mitosis, but in meiosis the two centromeres of each bivalent are already considerably separated.

(*c*) *Anaphase*. The centromeres continue to move apart in the direction of the poles of the spindle, dragging the chromatids with them.

(*d*) *Telophase*. Cytoplasmic cleavage occurs and the chromosomes may pass into the typical resting condition, a new nuclear membrane being reconstituted. At all events, it must be noted that there is now present, in each daughter nucleus, only the haploid number of chromosomes.

(2) Second Division

Unless the resting stages has intervened, the changes associated with prophase do not occur. Double threads appear, liberated into the spindle by the disintegration of the nuclear membrane (if reformed). Each component of every such double thread is a chromatid. The chromatids are nothing like as closely associated as they are in mitosis. Furthermore, as a result of chiasmata formation, they will not be genetically identical (see page 576). If for no other reason, this makes a second division essential to complete the process of meiosis. Each chromatid of every associated pair has a centromere of its own, by means of which it becomes attached in the equatorial plane of the nuclear spindle. With the separation of the chromatids, the reformation of nuclear membranes and the completion of cytoplasmic cleavage, two daughter cells are formed, each with the haploid number of chromatids. In the near future each chromatid splits longitudinally into two, thus forming a true chromosome.

Thus reduction in chromosome-number has been effected, since there is present now only the haploid number of chromosomes in each daughter-cell. This modified form of nuclear division differs fundamentally from mitosis in one respect, namely, that at the outset of the first meiotic division the chromosomes appear as single threads, and are not split longitudinally into component chromatids. At the anaphase of this same (first) division pairs of chromatids move to each pole, and not single ones, as in ordinary mitosis.

Gametogenesis

Though the occurrence of meiosis is believed to be universal in animals and plants where fusion of germ-cells occurs, it is peculiar amongst the Chordata owing to its accompaniment by other processes, differing in male and female. These processes, including amongst them meiosis, constitute the phenomenon of gametogenesis, further subdivided into spermatogenesis and oögenesis in male and female respectively.

(A) Spermatogenesis. Lining the tubules of the vertebrate testis are unspecialised cells, known as **spermatogonia**. These contain the diploid number of chromosomes, and divide by ordinary mitosis.

Eventually they give rise to cells which undergo division before their chromosomes have split longitudinally, and with homologous chromosomes lying side by side. These cells are the **primary spermatocytes**, and the division of each to form two **secondary spermatocytes** is evidently a first meiotic division. The second meiotic division is completed by each secondary spermatocyte to form two **spermatids**, each of which has now only the haploid number of chromosomes. A **spermatozoön** is formed from each spermatid by metamorphosis (a rapid series of changes) without further division. This metamorphosis involves the loss of almost all

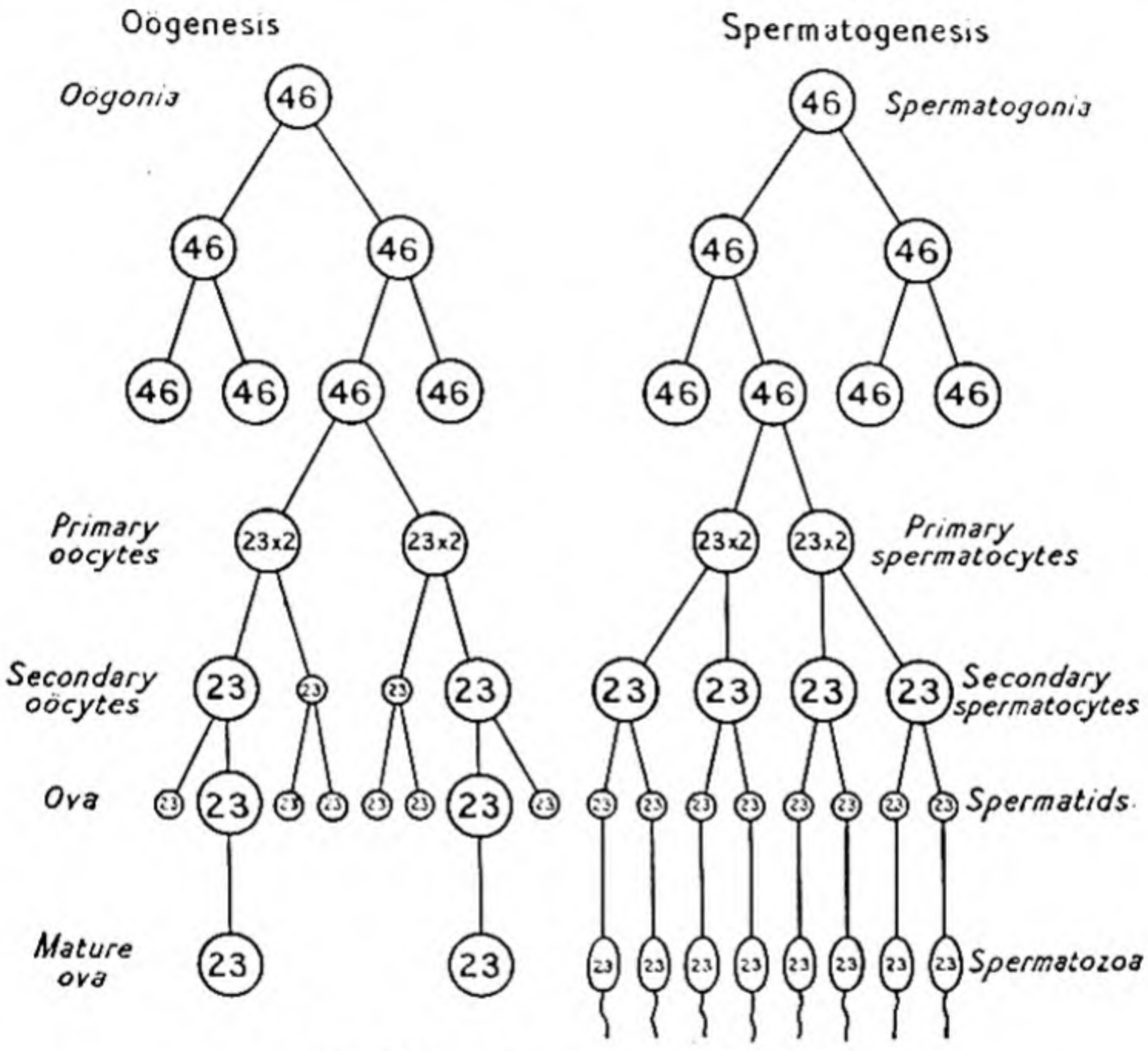


FIG. 211 – Gametogenesis in Man.
Note that in the female two of the 46 chromosomes will be *X*-chromosomes, whilst in the male one will be an *X*- and the other a *Y*-chromosome. (*See page* 580).

the cytoplasm except for a delicate filament forming the 'tail' of the spermatozoön, the 'head' of which is almost naked nucleus.

(B) OÖGENESIS. In the coelomic epithelium of the ovary lie cells known as **oögonia**. These correspond to the spermatogonia of the testis, and like them contain the diploid number of chromosomes and divide by ordinary mitosis. In further resemblance to the spermatogonia each eventually gives rise to two **primary oöcytes**, which exhibit the same

characteristics of an approaching first meiotic division as do the primary spermatocytes. By the completion of this division two similar nuclei are formed, but at this point there is an important difference observed between spermatogenesis and oögenesis. When a primary oöcyte divides cytoplasmic cleavage is very unequal, so much so that one of the nuclei acquires almost all the cytoplasm to form a **secondary oöcyte**, whilst the almost naked nucleus liberated at the same time constitutes the **first polar body**. The secondary oöcyte then undergoes the second meiotic division, and again cytoplasmic cleavage is unequal, resulting in the formation of one mature **ovum** and another almost naked nucleus, known this time as the **second polar body**. That the first polar body is, in effect, an abortive secondary oöcyte is evidenced by the fact that it itself frequently undergoes division to form two further second polar bodies. Thus from each primary oöcyte only one mature ovum is produced, whilst a primary spermatocyte gives rise to four spermatozoa.

The diagram on the previous page will serve to summarise nuclear behaviour at gametogenesis in man, where the diploid number of chromosomes is 46.

Meiosis in Plants

The stages of the life-cycle at which meiosis occurs in plants are discussed in Chapters 16 and 32. The problem is somewhat complicated by the fact that in the life-cycle of the majority of plants two distinct generations can be identified.

PRACTICAL WORK

Cell-division

Examine, under high power and oil-immersion, cells in a prepared slide of the growing point of a root or shoot. Look for cells in process of division and make out as many stages of mitosis as you can.

Gametogenesis

It is difficult to obtain practical details of oögenesis, but stages in spermatogenesis can be made out by minute examination of a prepared slide of a section of a vertebrate testis. Draw such stages as you can define.

CHAPTER 20

Tissue Elements of Higher Animals and Plants

A typical cell, such as described in Chapter 18, can hardly be said to exist at all in animals or plants, though some cells in certain organisms approximate to this structure. But the majority become modified and fulfil specific functions, usually to the exclusion of others. They may, for instance, serve for mechanical support, conduction of food-substances, or for protection. A **tissue** is the term applied to a collection of similar cells, all necessarily performing the same function, whilst an aggregation of cells more or less clearly separated from other structures in the body is called an **organ**. Thus a leaf of a tree and the heart of a frog are organs. An organ is frequently associated with more than one function – e.g., the vertebrate liver. Since the modes of life of animals and plants are different there must be corresponding differences in the types of cell comprising their bodies. Certain functions are common to both, however, and the cells accommodating them may well be compared, whilst cells effecting processes confined more or less exclusively to one or other of the two groups of living organisms must needs be described individually. For purposes of description a flowering plant and a typical vertebrate (*Rana* or *Oryctolagus*) will be considered.

Mechanical Tissues

Mechanical tissues are concerned with the support of the body, and in both animals and plants they are of several distinct types. A large part of the plant body, especially when young, consists of thin-walled, living cells, rectangular in shape, the length not greatly exceeding the width. These constitute a tissue known as the **parenchyma**. Plant storage-organs also consist largely of parenchyma. By a slight modification of the walls of parenchymatous cells a tissue known as **collenchyma**

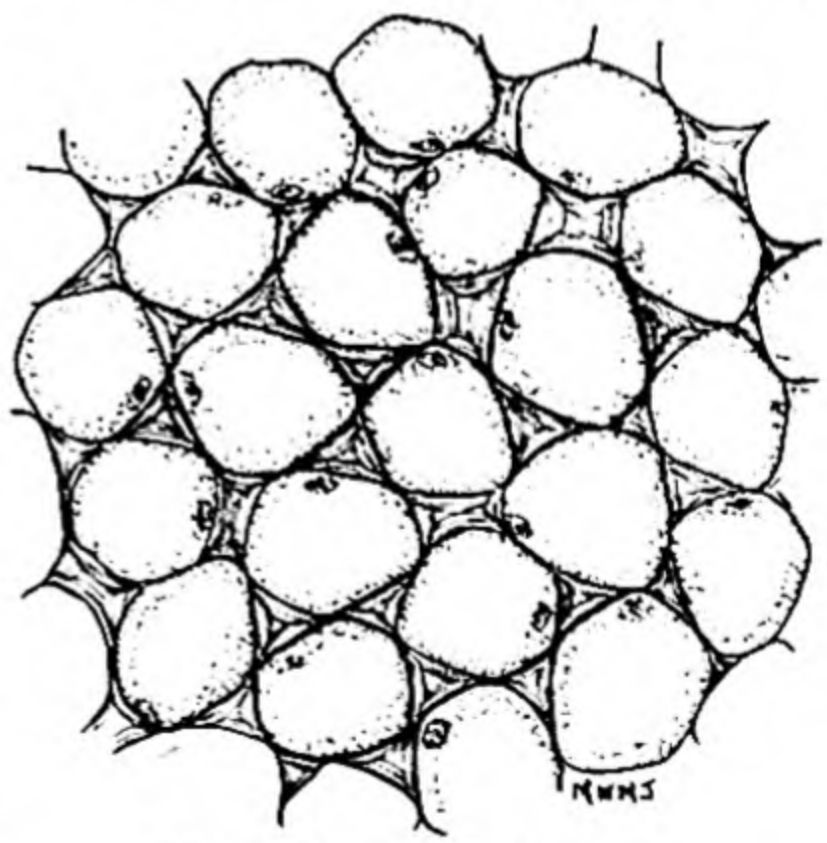


FIG. 212 – Collenchyma.

may be formed, the cells retaining their living contents, whilst the cellulose walls become thickened at the corners. Collenchyma occurs, for example, in the mid-ribs of young leaves. These two types of tissue afford a means of support, and yet do not render the plant too rigid. They may therefore be compared with connective tissue in the animal. At this point a very important feature may be observed, for, whilst plants are supported by actual cells, the mechanical support of animals is effected almost entirely by intercellular substance produced by certain cells. Thus **connective tissue** is largely concerned with binding up the various organs of the body into organic units. Thus the lungs, for example, as

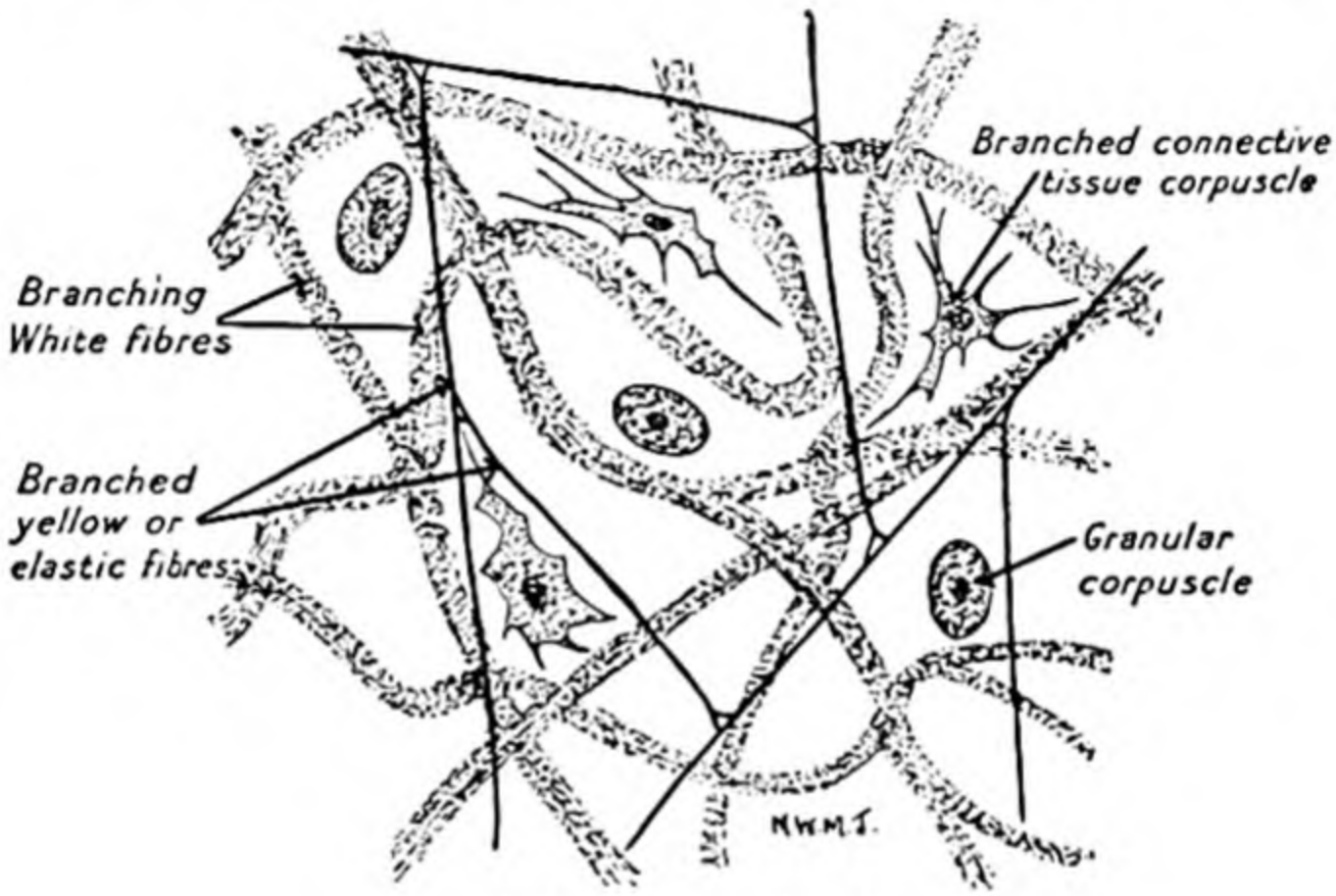


FIG. 213 – Connective tissue.

well as containing broncheoles, alveoli and blood-vessels, consist largely of connective tissue. There are three forms in which this tissue may occur.

(i) *Areolar Tissue*. This basic type of connective tissue consists of an admixture of all the essential ingredients of connective tissue and is widely dispersed throughout the body – e.g. the dermis of the skin. It is composed of a jelly-like matrix, thickly permeated by fibres, themselves of two sorts. The *white* fibres have a wavy outline, are composed of separate fibrils and resist stretching, whereas the *yellow* fibres are thin, straight and branching, rejoining to form a delicate network. They may readily be stretched. The two are differently constituted chemically. White fibres are composed of *collagen*, soluble in dilute acetic acid and yielding gelatin on boiling in water. Yellow fibres consist of *elastin*, which is both insoluble in water and also resistant to the action of acetic acid. The *fibroblasts* which secrete the white fibres are greatly elongated cells which lie in close contact with the fibres themselves, whilst those secreting the yellow fibres become isolated in the matrix.

In addition to the fibres and fibroblasts, the matrix also contains other types of cell. These include fat cells, found in groups and swelling greatly as fat accumulates within them. Where the amount of fat deposited is large the aggregate of cells constitutes *adipose* tissue. There are also present some white blood-corpuscles, known as *macrophages*, which may become phagocytic (page 328) to resist infection.

(ii) *White Fibrous Tissue.* As its name suggests, this tissue is a concentration of the white fibres found in areolar tissue, isolated from the other components. Bundles of such fibres constitute *tendons*, whose function it is to attach muscles to the periosteum (page 326) enclosing bones. Being inelastic they are able to transmit strains from one bone to another via a muscle.

(iii) *Yellow Elastic Tissue.* In contrast with the tendons described above, *ligaments* are composed of bundles of yellow fibres. They are largely concerned with the binding together of bones in such a way that joints are secure. Many of them, such as those on either side of the neck, are relatively large. Being elastic they do not impose too great a restraint on flexibility. Yellow elastic tissue is present in large amounts in the walls of arteries.

But the principal means of support, at any rate of older plants, is provided by **sclerenchyma** and the vessels of the xylem. Sclerenchyma consists of cells of two sorts, classified according to shape as *stone-cells* and *fibres*. The former are of parenchymatous shape, and occur, for example, in the flesh of some pears, rendering them gritty. Fibres are considerably elongated, a shape described as **prosenchymatous**. They occur plentifully in the cortex and wood of older plants, and are characterised by their great elasticity, yielding under stress, yet subsequently recovering their original size and shape. On this account flax fibres, for example, are used in the making of linen and lace. In this respect sclerenchyma differs from collenchyma, the latter being easily permanently stretched. Furthermore, whereas the walls of collenchymatous cells are of moderately pure cellulose, those of sclerenchyma become lignified (Chapter 18), and the living contents of the cell perish. In the walls of cells of sclerenchymatous tissue there

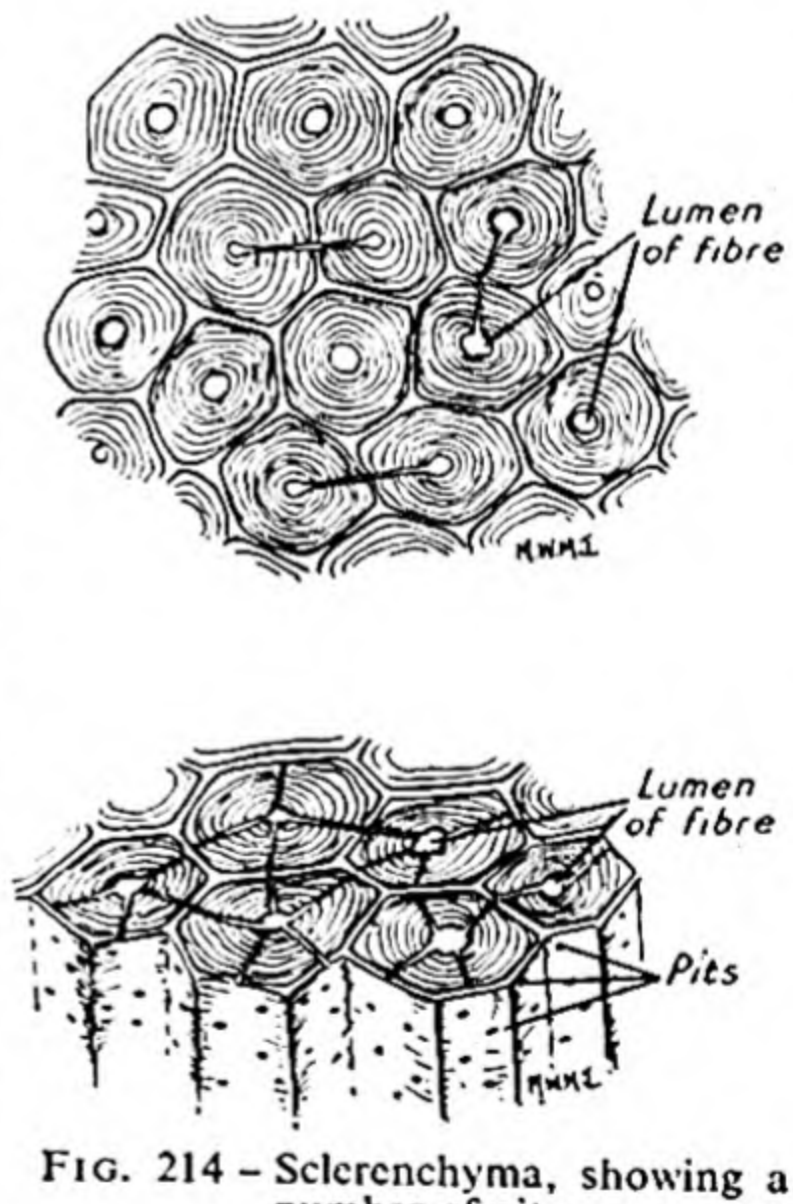


FIG. 214 – Sclerenchyma, showing a number of pits.

frequently appear regions where thickening has not taken place, and thus **pits** are formed. These afford a means of nutritive communication between adjacent cells prior to the completion of the thickening process. It may be pointed out here that the vessels, and to a greater extent the tracheids, of the xylem are also concerned in the mechanical support of the plant, but, since they are of primary importance as a conducting

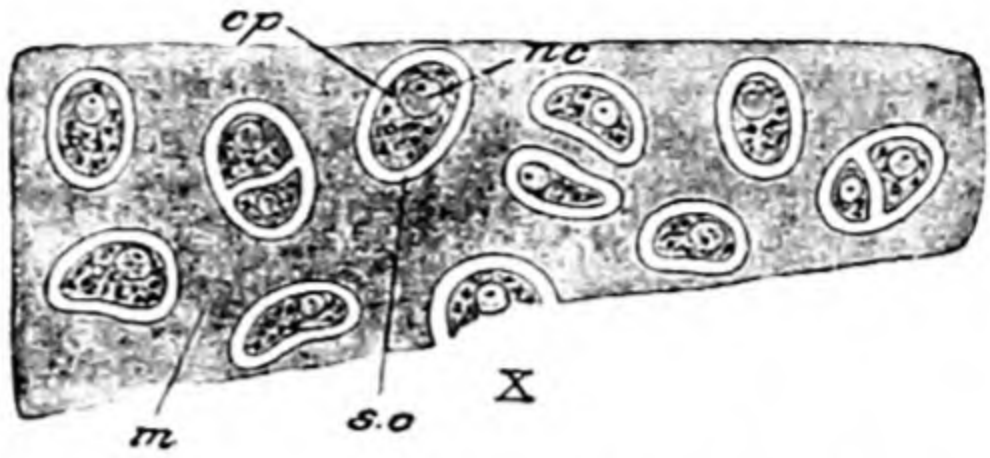


FIG. 215 – Hyaline cartilage. (From 'Atlas of Practical Elementary Zootomy', by G. B. Howes. Macmillan.)
cp., cartilage corpuscle; *m.*, matrix; *nc.*, nucleus; *sc.*, cell-space (lacuna).
The corpuscles are represented shrunk, as they most generally appear. In life they completely fill the lacunae.

medium, a detailed description will be reserved until conducting tissues are considered.

The main supporting tissues of vertebrate animals are cartilage (e.g., in the dogfish) and bone. **Cartilage** is the greyish, pliable tissue, popularly termed 'gristle'. The matrix is composed of *chondrin*, deposited by special cells. These cells are termed *chondroblasts* and themselves originate in the mesenchyme (page 518). As the cells complete their function they become enclosed in spaces – *lacunae* – in the matrix, either singly or in pairs, and are now known as *chondrocytes*. Any given cartilage is enclosed in an areolar tissue membrane, termed the *perichondrium*, which contains mesenchyme cells giving rise to more chondroblasts. Thus the cartilage increases in size by marginal extension. This is termed *appositional* growth, to distinguish it from *interstitial* growth, which continues in the substance of the cartilage. Near the margin of the cartilage the chondroblasts are in dense rows, parallel to the perichondrium. Within this area, in the zone where interstitial growth is continuing, they are irregularly disposed. Finally, in the centre, where the matrix is normally calcified, the mature chondrocytes are in columns at right angles to the surface. The cells themselves eventually die in this region. Cartilage contains no blood-vessels, but food supply for growth is reasonably ensured, since the matrix remains permeable to lymph.

In *hyaline* cartilage neither white nor yellow connective tissue fibres are present. It is found, for example, in the wall of the larynx and trachea, as well as which it is responsible for the attachment of the more

anterior ribs to the sternum, permitting some flexibility of the thoracic cage for the performance of ventilation movements.

Fibrous cartilage is characterised by the presence of white connective

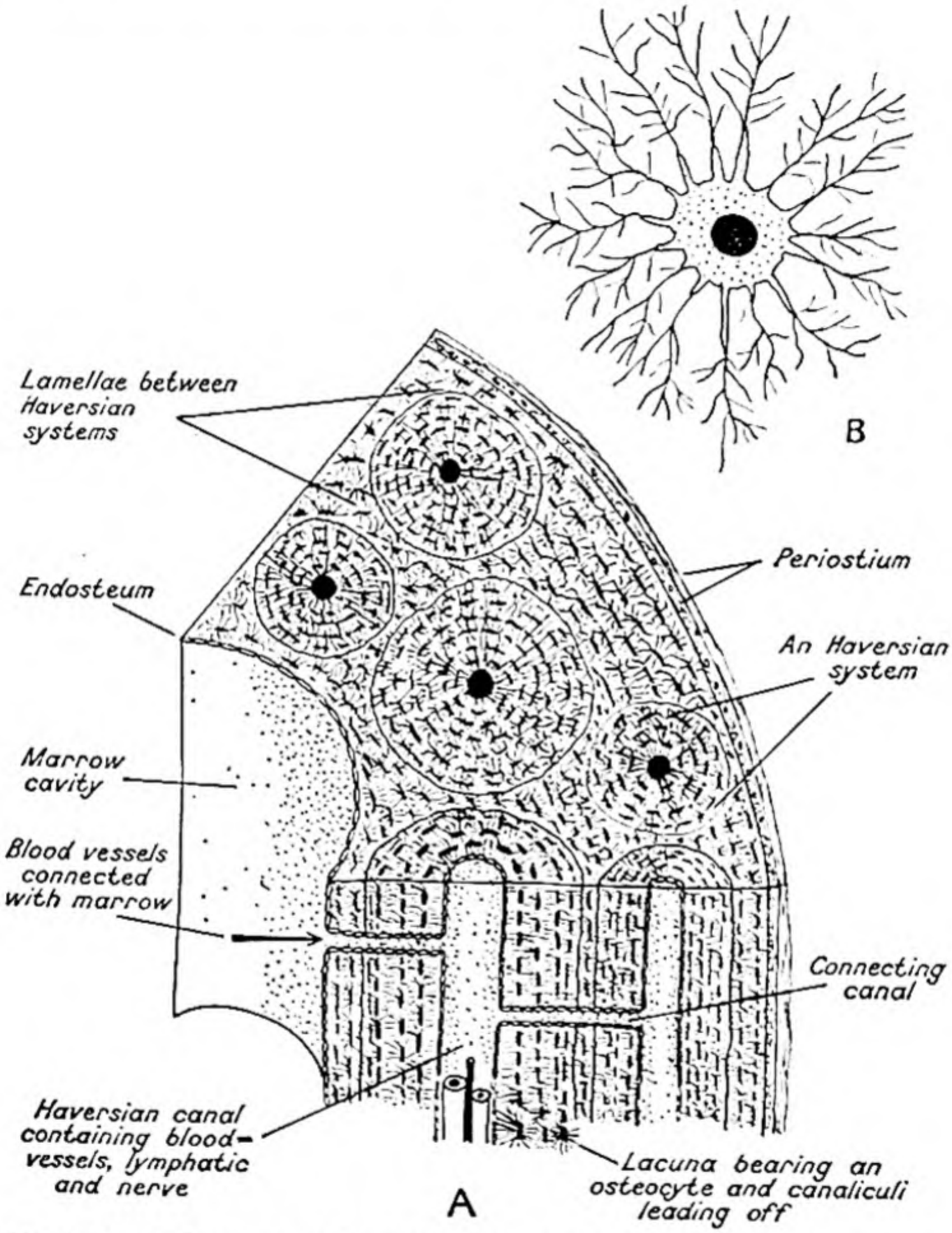


FIG. 216 – *A.*, Stereogram of a portion of a long bone; *B.*, A single osteocyte.

tissue fibres, making it the better able to resist pulls and tension. Intervertebral discs are formed of this type of cartilage.

Elastic cartilage, occurring, for example, in the epiglottis, in the pinna of the ear, and at the more distal end of the nose, owes its great flexibility to the presence of yellow connective tissue fibres. **Bone** differs from

cartilage in that the matrix, impermeable to lymph, always contains calcium salts, principally calcium phosphate, and the bone-cells are arranged in a regular pattern. The ground substance is arranged in cylinders, or *lamellae*, separated from each other by spaces known as *lacunae*, in which the actual bone corpuscles, or *osteocytes*, occur. In many bones, especially those of the limbs, there is a large, central *marrow-cavity*, around which the lamellae are set. There are present also smaller channels, known as *Haversian canals*, around which

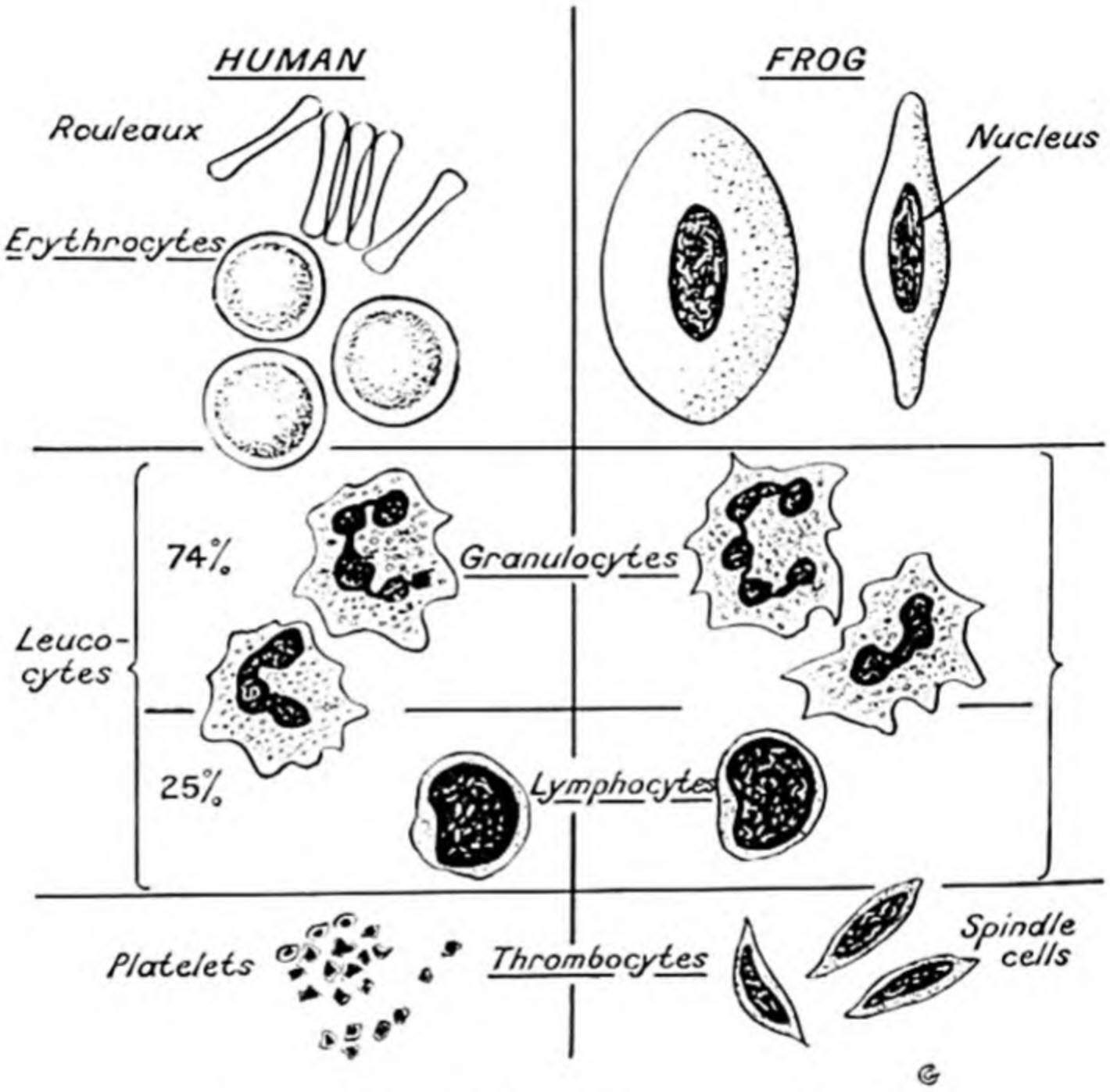


FIG. 217 – Principal types of blood-corpuscle.

are grouped further lamellae. The lacunae are connected with each other by *canaliculi*, running in the ground-substance. The ground-substance of cartilage and bone differs from that of connective tissue in that the former, on boiling, yields *chondrin*, and the latter *gelatin*, each a product of protein hydrolysis. Corresponding to the perichondrium of cartilage, every bone is enclosed within a connective tissue membrane, known as the *periosteum* (page 549).

An appreciable degree of support, both in animals and plants, is effected by the pressure of the liquids which they contain. The living cells of the plant body are said to be turgid when fully distended with sap,

and the importance of this will be realised when it is remembered how a plant wilts as a result of water-shortage. In animals it is not so much the fluid in the individual cells that affords support as the pressure of blood, especially in the arteries. Accordingly, **blood** may be classed as a skeletal tissue, and like others it is characterised by the enormous amount of inter-cellular substance, this time a liquid and known as the *plasma*. This plasma, however, differs from the inter-cellular substance of other skeletal tissues in that it is not secreted by the blood-corpuscles. It is a pale straw-coloured liquid, consisting of an aqueous solution of salts and organic substances. The principal salts present are sodium chloride and bicarbonate, together with the sulphates and phosphates of sodium and potassium. Food-substances in the form of glucose and amino-acids are carried in solution, as is the waste-product, urea (or some closely allied compound). Proteins are also present in colloidal solution, including albumins, globulins and fibrinogen, the last-named being associated with clotting. Fat droplets may also occur. In addition to the above substances, all susceptible to qualitative analysis, the presence may also be demonstrated, by physiological means, of hormones (page 479) and anti-toxins (page 357).

The red corpuscles, or **erythrocytes**, in man are biconcave, enucleate discs, about $7{\cdot}5\mu$ in diameter and 2μ thick in the centre. Each is enclosed within a very thin, elastic envelope, consisting of an outer lipoid layer, lined with a rather thicker layer of protein molecules radiating from the centre, like the spokes of a wheel. It is probably to this layer that the erythrocytes owe their elastic nature, a quality of great importance in facilitating their passage through capillaries. The centre is filled with homogeneous cytoplasm, in which is dissolved *haemoglobin* (page 434). There are some five million erythrocytes per cubic millimetre of blood, with rather less in the female. When removed and stationary they tend to adhere, like a pile of plates, to form *rouleaux*. Their vast number and flat shape ensure a large surface-area for the absorption of oxygen.

Erythrocytes are formed at the rate of about one million per second in the red marrow of the bones, especially those of the skull and the vertebrae, from cells termed *erythroblasts*. They have an active life of about three months, after which they are destroyed at the same rate by phagocytosis (page 328) in the spleen and liver. Following the decomposition of the haemoglobin, much of the iron is retained for further use, whilst the remainder of the molecule is converted into the bile pigment, *bilirubin*, being eliminated through the intestine, imparting the characteristic colour to the faeces.

Leucocytes, or white (colourless) corpuscles, are classified into two major groups according to the nature of their cytoplasm. Each group is further subdivided on other characteristics, as indicated below.

(*a*) *Agranulocytes*. Here the cytoplasm remains relatively free from granulation. There are two types. The *lymphocytes* are about the size of

an erythrocyte and possess a large, rounded nucleus. They comprise up to 25% of the total leucocyte content of the blood and may well be concerned with detoxication (page 344), for the number increases during infection. *Monocytes* are larger but much less numerous. Each is about 20μ in diameter and contains a bean-shaped nucleus. Monocytes may possibly be concerned with the formation of anti-bodies (page 357).

(*b*) *Granulocytes*. In these the cytoplasm is granular and the nucleus lobed. They are further classified according to the staining reaction of their cytoplasm into *neutrophils* (trilobed nucleus; stain with neutral dyes; about 8μ in diameter; comprise over 70% of all leucocytes), *eosinophils* (large, rounded granules in the cytoplasm, which is itself stained pink by such acid stains as eosin; about 10μ in diameter; about 2% of the total) and *basophils* (granules stain purple with Leishman's stain; nucleus bilobed; less than 1% of total).

To members of the three classes of granulocytes various functions are attributed. The neutrophils are *the* phagocytes of the blood (see below) and are said to be able to secrete enzymes to assist in the digestion of dead tissues. Eosinophils are claimed to be especially numerous in sufferers from allergies, for which they are possibly responsible. They are thought to combat the formation of histamines by the interaction of antibodies and antigens. The function of basophils is uncertain.

The total number of leucocytes per cubic millimetre of blood varies between five and nine thousand. They are characterised by their great mobility and are as numerous outside the blood as within it. One of their principal functions is phagocytosis. This is the ingestion of foreign particles, including bacteria, and hence they have a highly significant protective function. Large local accumulations of them in an albuminous fluid constitute pus. Lymphocytes are formed in lymphoid tissue and in particular at the lymph nodes, whilst granulocytes are produced in the red marrow of the bones. They are destroyed in the liver in the same way as erythrocytes, whilst many of them merely degenerate in the lymphoid tissue. Leucocytes have an average life of about twenty-four hours.

Platelets are minute, enucleate discs, of diameter about 3μ. They are believed to be derived from large cells, known as *megakaryocytes*, in the liver, portions becoming detached and floating off into the blood. Some authorities believe that the platelets of mammals are not represented in other vertebrates, being substituted by nucleate, spindle-shaped cells, which also play a part in the clotting of the blood. In mammals there are some two to three hundred thousand per cubic millimetre of blood and they have an active life of about one week. Their function in connexion with clotting is described on page 356.

Surface Tissues

The function of cells comprising an external surface is obviously one of protection. In plants the cells of the superficial layer, or **epidermis**, are

characterised by the formation of a layer of *cutin* over their outer surface. Unlike normal thickening this cutin is deposited on the *outside* of the primary cell-wall, and is impermeable to water. In animals surface tissues are termed **epithelia**, although those lining a cavity – i.e. providing an internal surface – are often referred to as **endothelia**. In the following description the term 'epithelium' will be used to embrace both types. Epithelia are themselves classified, somewhat irrationally, on a mixed basis of form and function. Thus they may be *simple* (one layer of cells thick) or *stratified* (several cells thick). The former may be columnar, ciliated, pavement or cubical, according to the form of the cell, whilst

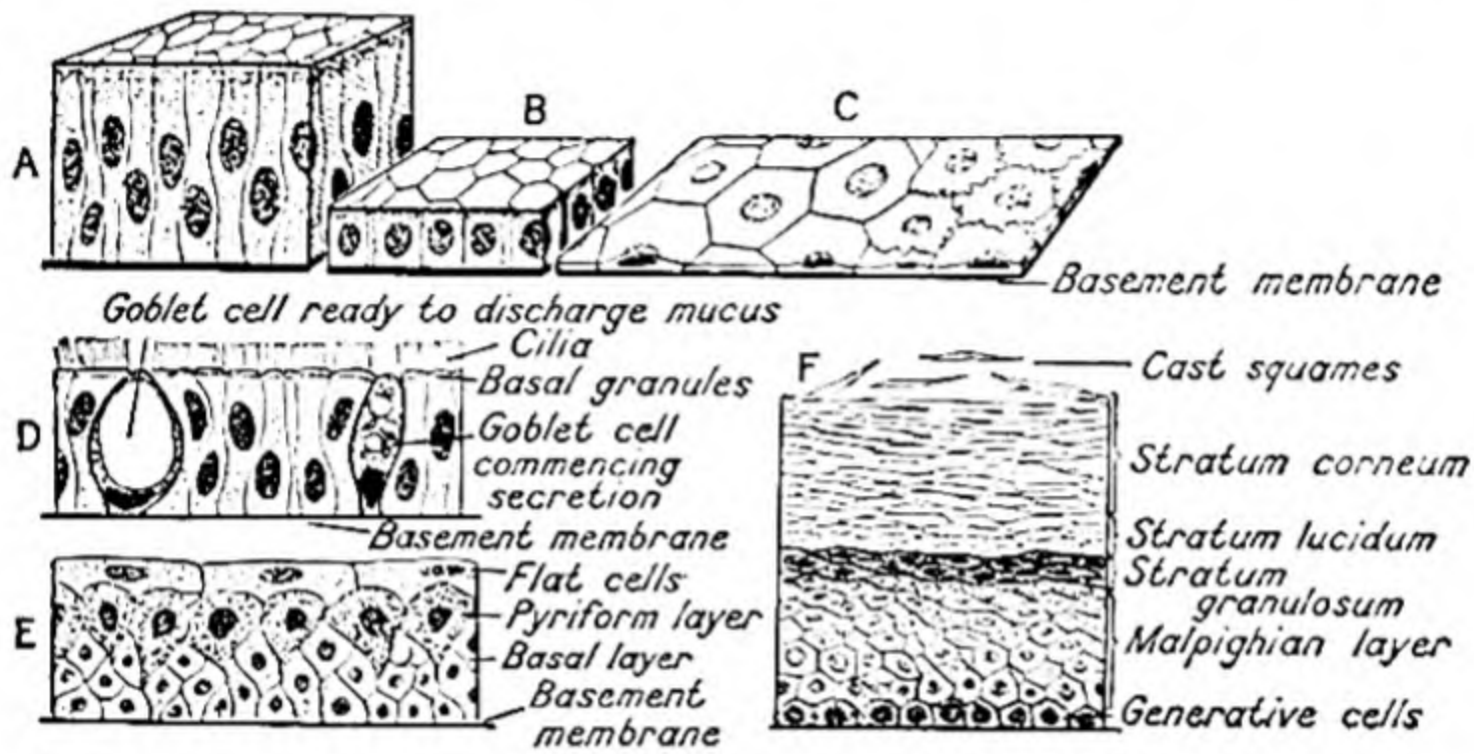


FIG. 218 – Main types of vertebrate epithelium.
A., Columnar; *B.*, Cubical; *C.*, Pavement (squamous), with the tesselated variety to the right; *D.*, Ciliated; *E.*, Transitional; *F.*, Stratified (squamous type).
Examples – A., Intestine; *B.*, Ducts of glands; *C.*, Lining of coelom, air sacs and blood-vessels; *D.*, Trachea, buccal cavity of frog; *E.*, Mammalian bladder only; *F.*, Vertebrate skin only.

the glandular type is distinguished functionally. It is, in fact, not unusual for the cells of glandular epithelium to be of columnar type. All types, however, share the basic property of being composed of sheets of cells, joined together (or separated, depending on the point of view) by layers of intercellular substance. Furthermore, in the vast majority of cases, the cells rest upon a continuous *basement membrane*, derived either from the cells themselves or from the underlying tissues. The membrane itself is amorphous and supported by a network of fibres. The various types of simple epithelium will be described individually in outline.

(i) *Columnar.* Here the cells are greatly elongated at right angles to the surface of the layer. Adjacent cells are frequently joined by delicate cytoplasmic threads. This type of epithelium (endothelium) is to be found, for example, lining the greater part of the gut.

(ii) *Ciliated.* The cells are frequently columnar in form, but are charac-

terised by the presence, on their free surfaces, of delicate, vibrative, cytoplasmic projections, or *cilia*. Each consists of a number of discrete threads, whilst at its base is a single or double granule, associated with its activity. Tracts of such cells work on a co-ordinated pattern, reminiscent of the metachronal rhythm already instanced in *Paramecium* (page 10). They may be found, for example, in the nasal cavities, trachea and bronchi, where, with the aid of mucus, they drive foreign particles, trapped in the mucus, away from the lungs. They occur also in the epididymis, the Fallopian tube and superficially on the tadpole at the time of hatching. Their importance in *Branchiostoma* is described on page 506.

(iii) *Pavement*. This type, known also as *squamous*, is composed of cells flattened out upon the surface covered to such an extent that the nucleus of each cell may cause it to bulge. The cell-outlines are frequently wavy, in which case the epithelium is described as *tesselated*, and such is the case with the lining layer of blood-vessels. Pavement endothelium occurs also in the Bowman's capsules of the kidney (for filtration), in the alveoli of the lung (for diffusion) and in the peritoneum (for smoothness).

(iv) *Cubical*. This is roughly intermediate between the columnar and pavement types, for the cells, although not flat, as in pavement, are not as elongated as in columnar. This type is found, for example, in uriniferous tubules and in the thryoid and sweat glands.

(v) *Glandular*. A final type of cell constituting a simple endothelium in animals makes its appearance also in the plant body. It is the *gland-cell*, associated with the elaboration of specific chemical substances. In plants such cells are usually found in isolation, or small groups may occur together. Examples are afforded by the cells lining the nectaries of flowers and producing nectar, as well as by certain cells in seeds and parts of the plant body where enzymes are formed. In insectivorous plants enzymes are produced for the solution of the body-substance of the captured prey. Mineral salts are secreted by some plant cells. Thus silica is deposited in the outer layers of grasses, accounting for their sharp, cutting edge. Similarly in certain non-cellular Algae, known as Diatoms, silica is laid down. Cells of some plants become encrusted with calcium carbonate, as seen in some stoneworts, whilst in certain cells of the outer layers of the leaves of stinging nettles aggregations of calcium carbonate, known as *cystoliths*, occur. In higher animals, the cells of glandular endothelium are columnar or cubical in form, but are specialised functionally. This applies to many of the cells lining the alimentary canal, including the stomach, all of these being columnar. Cells secreting mucus, which is passed up to the surface, are often termed *goblet cells*, from their characteristic shape.

Although there is nothing especially distinctive about gland cells in respect of their visible structure, they are associated together in divers ways to constitute the functional component of glands. Based upon this

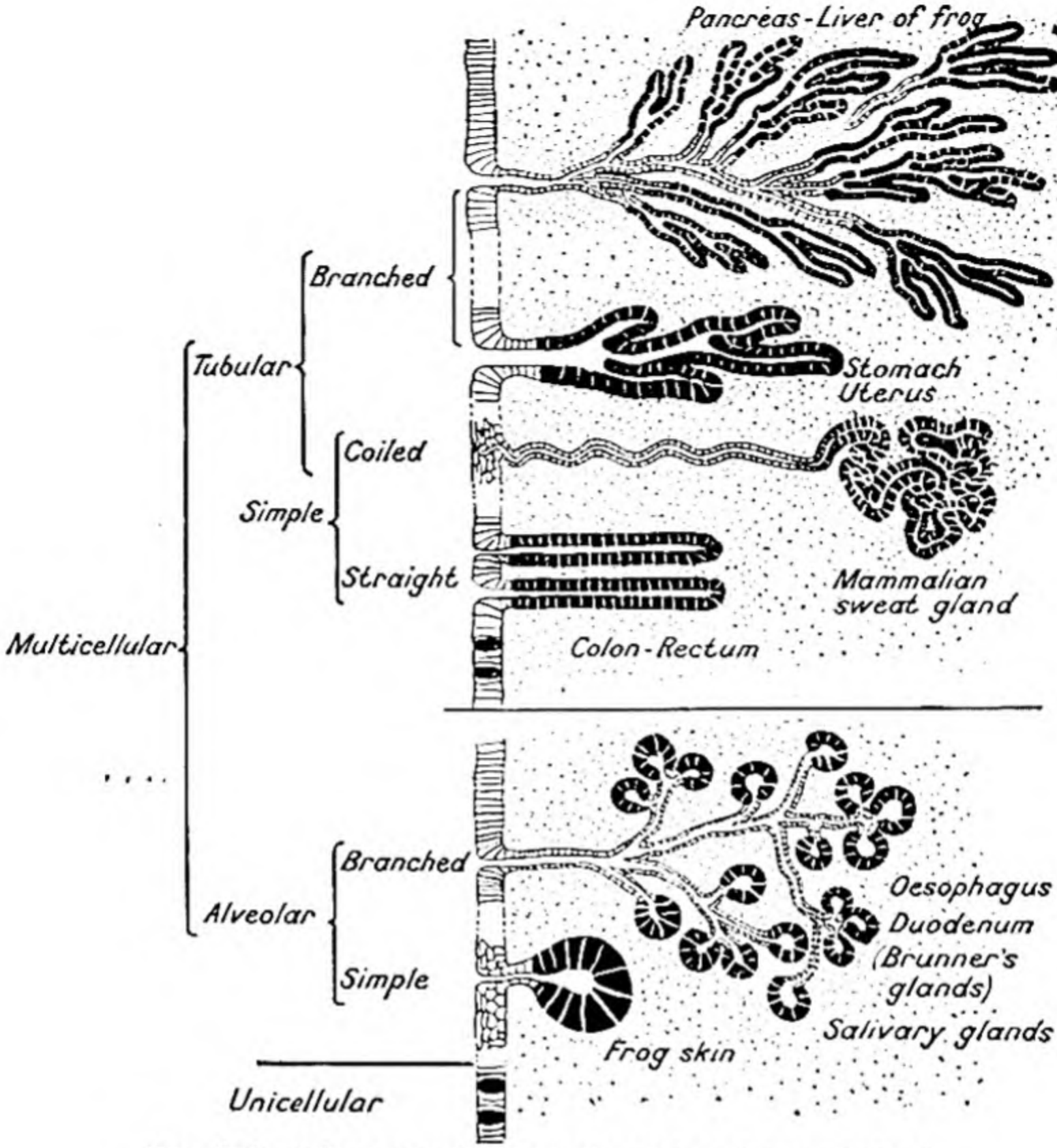


FIG. 219 – Diagram to illustrate the various forms of gland.

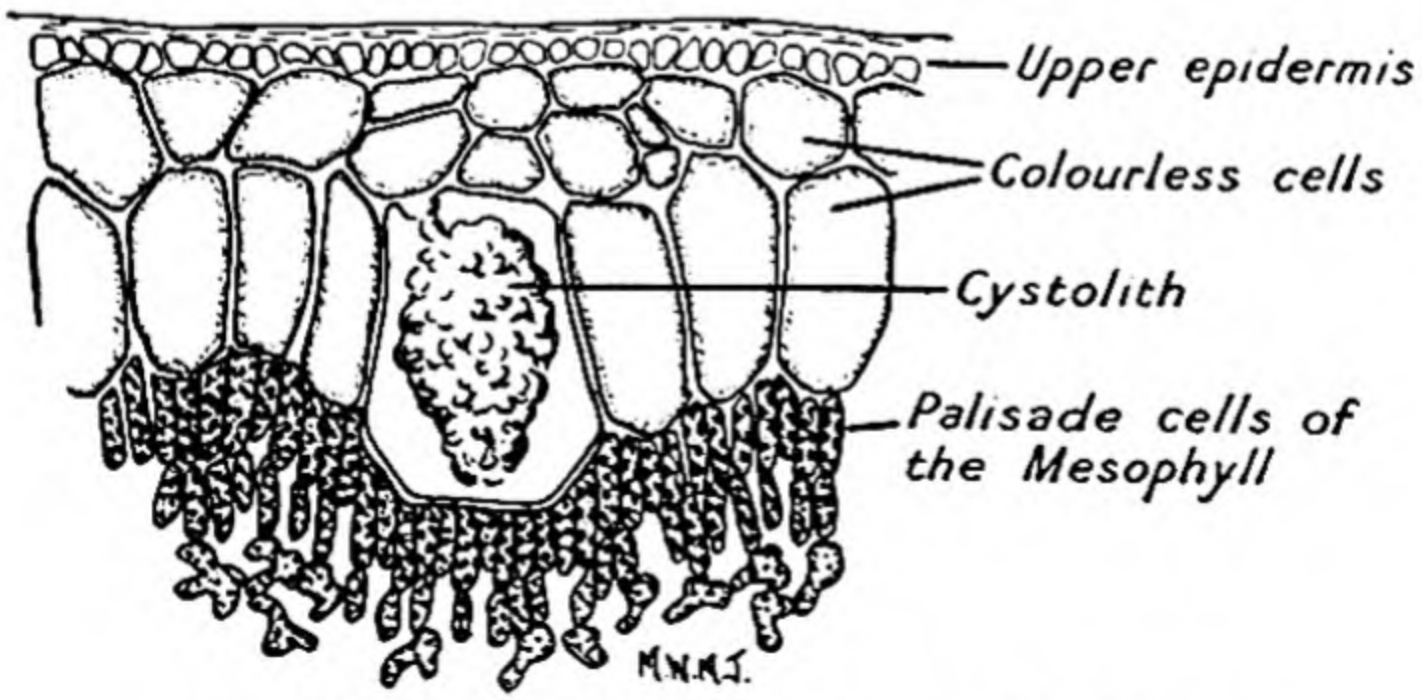


FIG. 220 – A cystolith in a leaf of the Stinging Nettle.

arrangement, glands may be classified into a number of categories. Most glands possess ducts, charged with the function of conveying the products of secretion to a specific field of action. Thus the ducts of the salivary glands open into the buccal cavity, and that of the pancreas into the duodenum. Such glands are described as **exocrine**. Other glands possess no associated ducts. These are **endocrine** glands, exemplified by the thyroid and the pituitary. Their secretions, termed hormones (Chapter 27), escape by diffusion from the secretory components of the glands and by the same physical process enter the bloodstream through the walls of the capillaries for distribution.

Glands are further classifiable according to the scheme outlined below, based, as it is, on the form of the functional units of the gland.

(A) TUBULAR GLANDS. In these, the terminal portion of the gland is cylindrical.

(*a*) *Simple*. The gland is composed of a single unit, which may be:

(i) *Straight* – e.g. crypts of Lieberkühn (page 440).

(ii) *Coiled* – e.g. sweat glands (page 141).

(iii) *Branched* – e.g. in the lining of the uterus.

(*b*) *Compound*. The gland is composed of many units – e.g. kidney.

(B) ALVEOLAR GLANDS. In these, the terminal portion is enlarged, becoming spherical or oval.

(*a*) *Simple*. One unit only is present – e.g. mucous gland of skin of frog.

(*b*) *Compound*. Many units compose each gland – e.g. salivary gland.

It will be realised that the simple types of epithelium described above cover internal surfaces. There is little internal surface in the majority of plants, the body being relatively compact and the spaces small. The only internal surface of importance is that afforded by the spongy tissue of the leaf, the cells here being of the ordinary parenchymatous variety, irregularly arranged so as to enclose spaces. Aquatic plants frequently have a large internal surface, since they are extensively penetrated by spaces, thus rendering them more buoyant. Land plants with hollow stems and petioles are not uncommon. In either case the lining is largely provided by parenchymatous tissue. Important gland-cells, as in animals, are those secreting hormones (Chapter 27).

Returning to animals, stratified epithelium is exemplified by the epidermis of the skin, stomodaeum and proctodaeum (page 72). This organ (for the skin fulfils all the necessary conditions for it to be so classified) has already been described in dogfish (page 83), frog (page 111) and mammal (page 140). The innermost layer of the stratum Malpighi, resting upon the basement membrane, consists of roughly spherical cells, which, by repeated division, maintain the more superficial layers, where friction may take its toll. The strata lucida and granulosa, already referred to on page 140, are in the transitional stages of compression and

death, whilst the stratum corneum consists of horny plates, the last remains of these cells. This layer provides protection against desiccation.

Intermediate between simple and stratified is a type of epithelium which, although more than one layer thick, differs from the genuine stratified type in that the cells are far from uniform in size and are not arranged in definite layers. It does not undergo continuous growth. The cells can be moved relative to one another and thus the epithelium itself can be stretched, accompanied by thinning. It is found, for example, in the urinary bladder, thus allowing for the accumulation of urine.

The remaining tissues of animals and plants must be described separately. Muscular and nervous tissues are obviously not represented in plants, whilst, though conduction of food-substances occurs in both types of organism, the conducting tissues of plants consist of special kinds of cell, whereas the arteries and veins, effecting such conduction in animals, are really composite structures, consisting of endothelium, muscular and connective tissues (see page 322).

Muscular Tissues of Animals

The cells comprising muscular tissues have become specialised in their immense powers of contraction, this involving only a change of shape and not of volume. There are three types, known respectively as striped, unstriped and cardiac.

STRIPED MUSCLE. This is composed of fibres large enough to be visible to the naked eye. Each fibre is cylindrical for the greater part of its length, with a diameter of about 50μ, tapering at either end. It is invested in a thin membrane, known as a **sarcolemma**, within which is a mass of special contractile cytoplasm, known as **sarcoplasm**. Many nuclei occur superficially, so that the entire fibre is a *coenocyte*, or *syncitium* – i.e. a continuous, multinucleate mass of protoplasm, not divided by cell-walls. The centre of the fibre consists of bundles of longitudinal **myofibrillae**, each zonally differentiated on a complex pattern. Thus at intervals black discs (*A discs*) lie transversely, separating lighter-coloured zones (*J discs*) but not quite reaching the margin of the myofibrilla. Since the discs occur at the same levels in all the component myofibrillae of a single fibre, the impression is created of a series of closely packed dots across the entire width. More detailed optical analysis reveals that each *J* disc is traversed by a very thin *Z* line. These are continuous from one myofibrilla to another and finally with the sarcolemma of the fibre. In the relaxed state the *A* discs have been observed each to be divided transversely by a light-coloured *M* line.

An entire muscle is composed of fibres, arranged in bundles (*fasciculi*). Connective tissue plays an important packing role. Thus each fibre is invested in an *endomysium*, each fasciculus in a *perimysium* and the whole muscle in an *epimysium*.

Since striped muscles can be contracted at will, they are described as

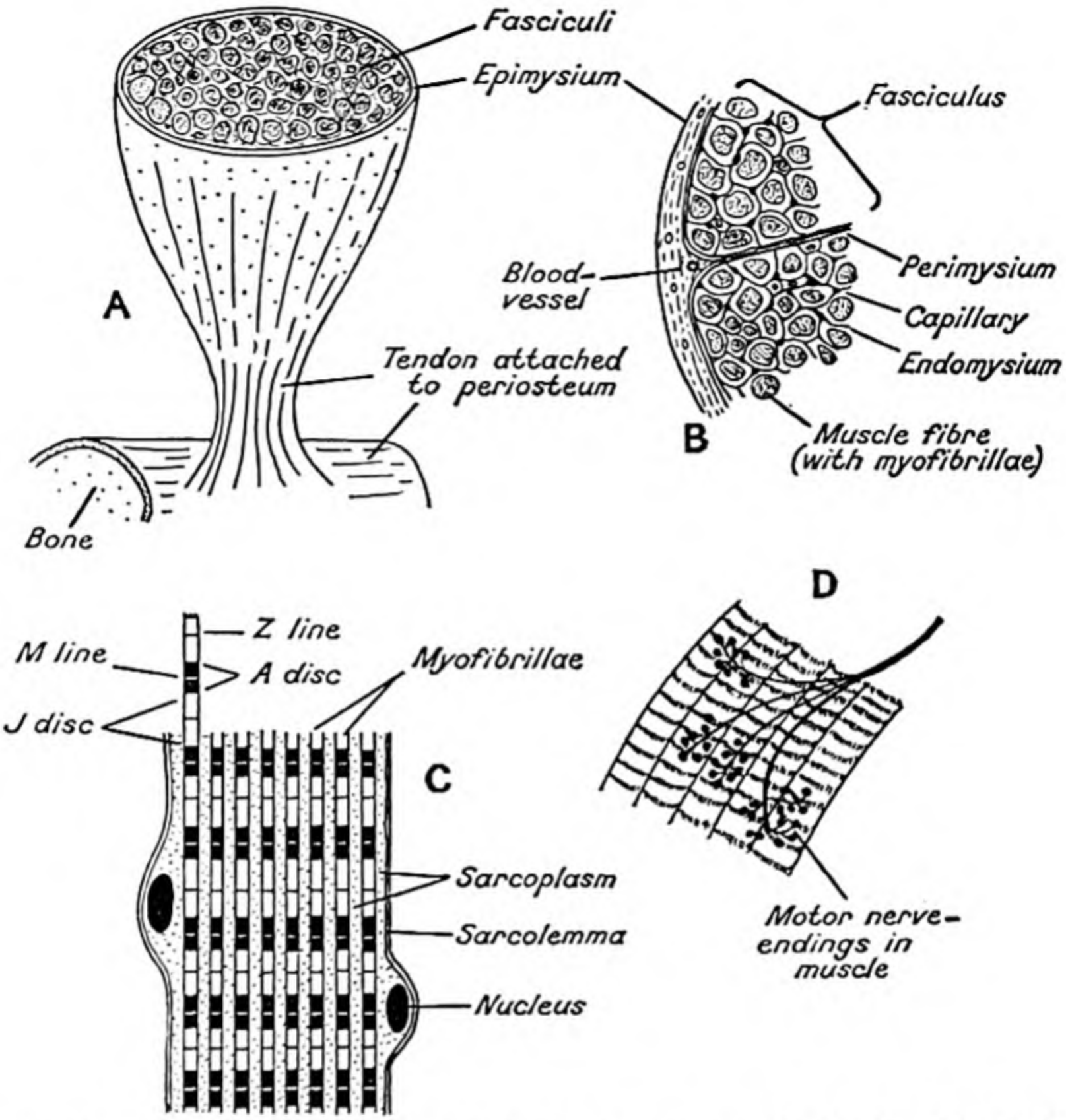


FIG. 221. *A.*, Transverse section through a voluntary muscle, also showing attachment to bone; *B.*, Transverse section through a muscle (higher magnification); *C.*, Part of a muscle fibre, highly magnified; *D.*, Motor nerve-endings in muscle.

voluntary and are exemplified by the muscles responsible for the movement of the limbs, the eyes, the diaphragm and the tongue.

UNSTRIPED MUSCLE. This consists of uni-nucleate, spindle-shaped cells, varying in length from 20μ to 0·5 mm., found respectively, for example, in blood-vessels and a pregnant uterus. The majority of the cell is composed of longitudinal myofibrillae, whilst the centre is occupied by the nucleus, enclosed within a mass of sarcoplasm. There is no sarcolemma, whilst adjacent cells are united by delicate connective tissue fibres.

Since most unstriped muscle is not susceptible to the control of the will, it is described as *involuntary*. It is this type of muscle which occurs,

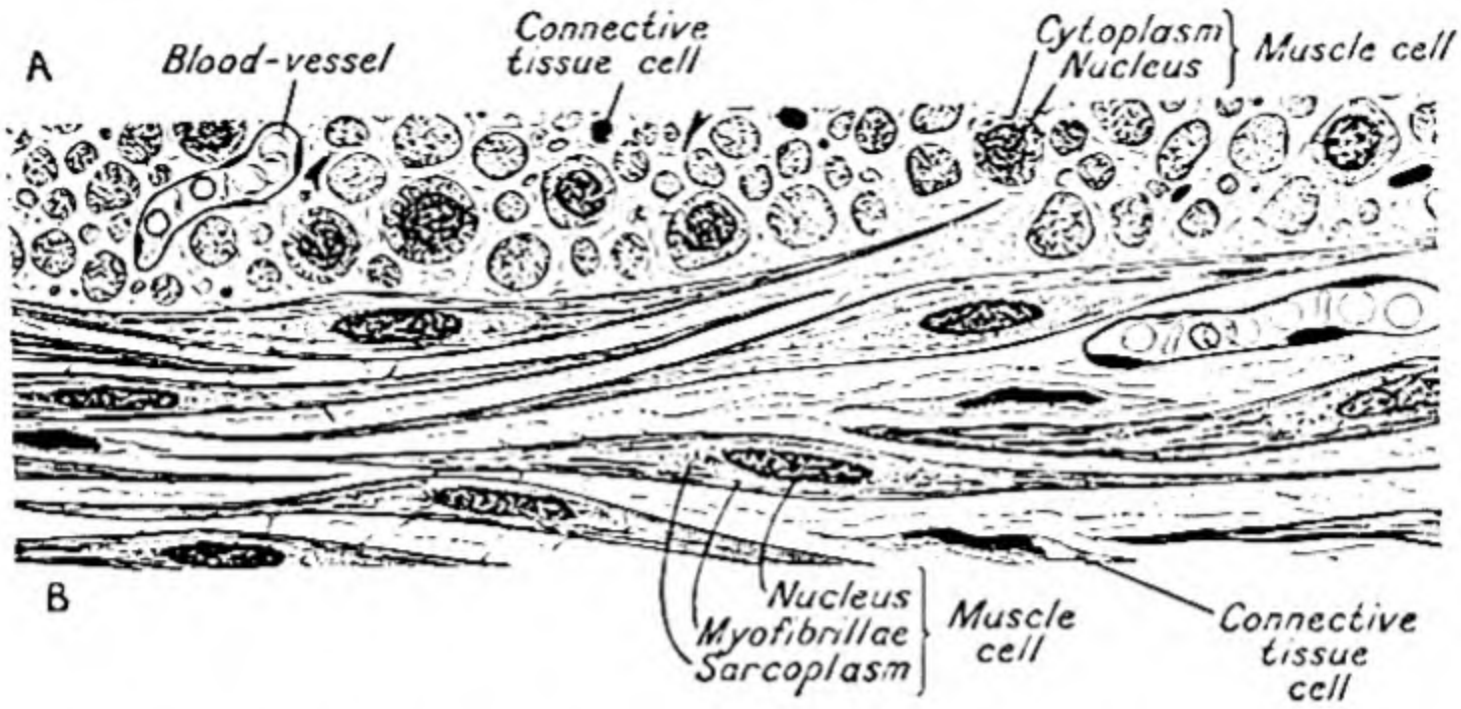


FIG. 222 – Unstriped (involuntary) muscle.
A., Muscle cells seen in cross section; *B.*, Lateral view of a number of cells.

for example, in the wall of the alimentary canal, the uterus, the bladder and blood-vessels.

CARDIAC MUSCLE. This, as its name implies, is confined to the wall of the heart. In structure it is roughly intermediate between the two types already described. Thus, as in striped muscle, the fibres are cylindrical, but they branch repeatedly to form a network, with branches from neighbouring fibres uniting. Each fibre contains a central nucleus, surrounded by sarcoplasm. Myofibrillae show some transverse markings. The most important of these are the *intercalated discs*, formed by the inward extension of the sarcolemma across the fibre, which they thus divide into separate cells. Cardiac muscle differs from both the striped and the unstriped varieties in that its contraction is not dependent upon nervous stimulation, but is rhythmic. It is also immune to fatigue and tetanus. Only the speed of heart-beat is subject to nervous regulation. It is interesting to note that the rhythmic beating of the heart of a foetus is established before nerve-fibres reach it.

Nervous Tissues of Animals

Nerve-cells, or **neurones**, are specialised for excitability and for the conduction of impulses from one part of the body to another. It is therefore to their advantage in this respect to have one or more elongated processes emanating from the mass of the cell, thus avoiding the frequent transference of impulses from one cell to another. Accordingly, a nerve-cell is found to consist of a very much branched cell-body, containing numerous dark-staining Nissl granules and a single nucleus, whilst the branches are known as *dendrites*. The Nissl granules are composed of nucleo-protein, and contain iron. They disintegrate and eventually disappear after prolonged activity of the nerve-cells, or after contact with poisons which act primarily on the nervous system. The

cytoplasm also contains delicate **neurofibrillae**, some of which appear to extend into the various projections of the cell-body. Any very much elongated process emanating from the cell-body is either a **dendron** or an **axon**, the former conducting impulses to the cell-body and the latter away from it. In either case it becomes considerably subdivided at its free end to form the *terminal arborisation*. Covering the nerve-fibre is a delicate membrane, known as the *neurilemma*, composed of a series of drain-pipe cells and beneath which occurs a number of nuclei, one to each

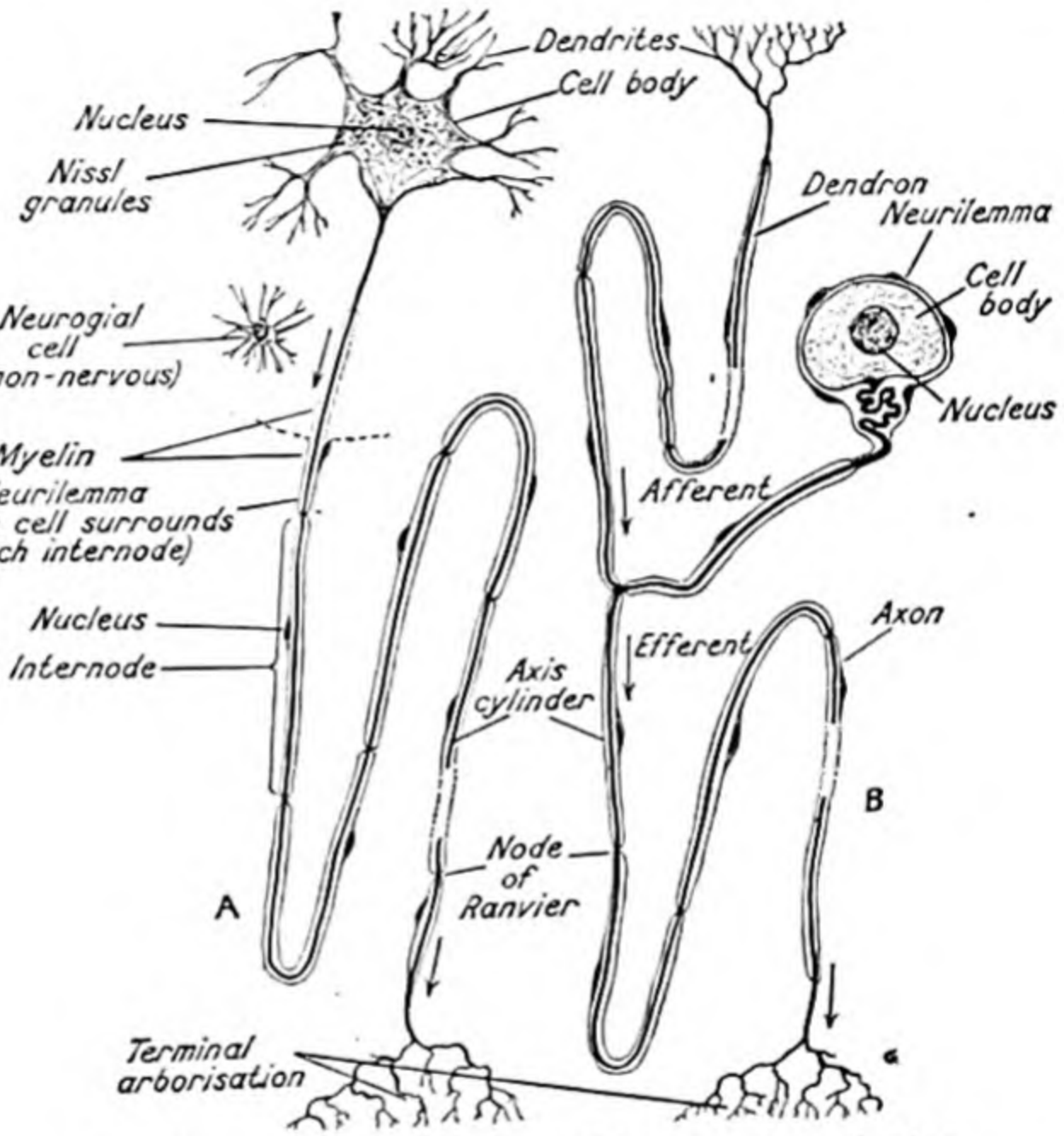


FIG. 223 – Nerve cells. *A.*, Multipolar; *B.*, Unipolar.

inter-node. The neurilemma is present only on those parts of nerve-fibres outside the brain and spinal cord. Nerve-fibres are of two sorts, medullated and non-medullated. In the former the axon itself is separated from the neurilemma by a layer of fatty material, known as the *myelin sheath*. This is constricted at intervals to form the *nodes of Ranvier*. In the non-medullated fibres this myelin sheath is absent. The medullated fibres occur in the brain, spinal cord, and cranial and spinal nerves, whilst the non-medullated variety is confined to the autonomic nervous system. Nerves are formed by many fibres, bound together in a connective tissue sheath – the *perineurium* – and the whole bundle enclosed within a further sheath – the *epineurium*. Interspersed with the nerve-cells are un-

differentiated supporting cells, termed *neuroglia*. The area of transfer of an impulse from one nerve-cell to another is termed a **synapse** (see

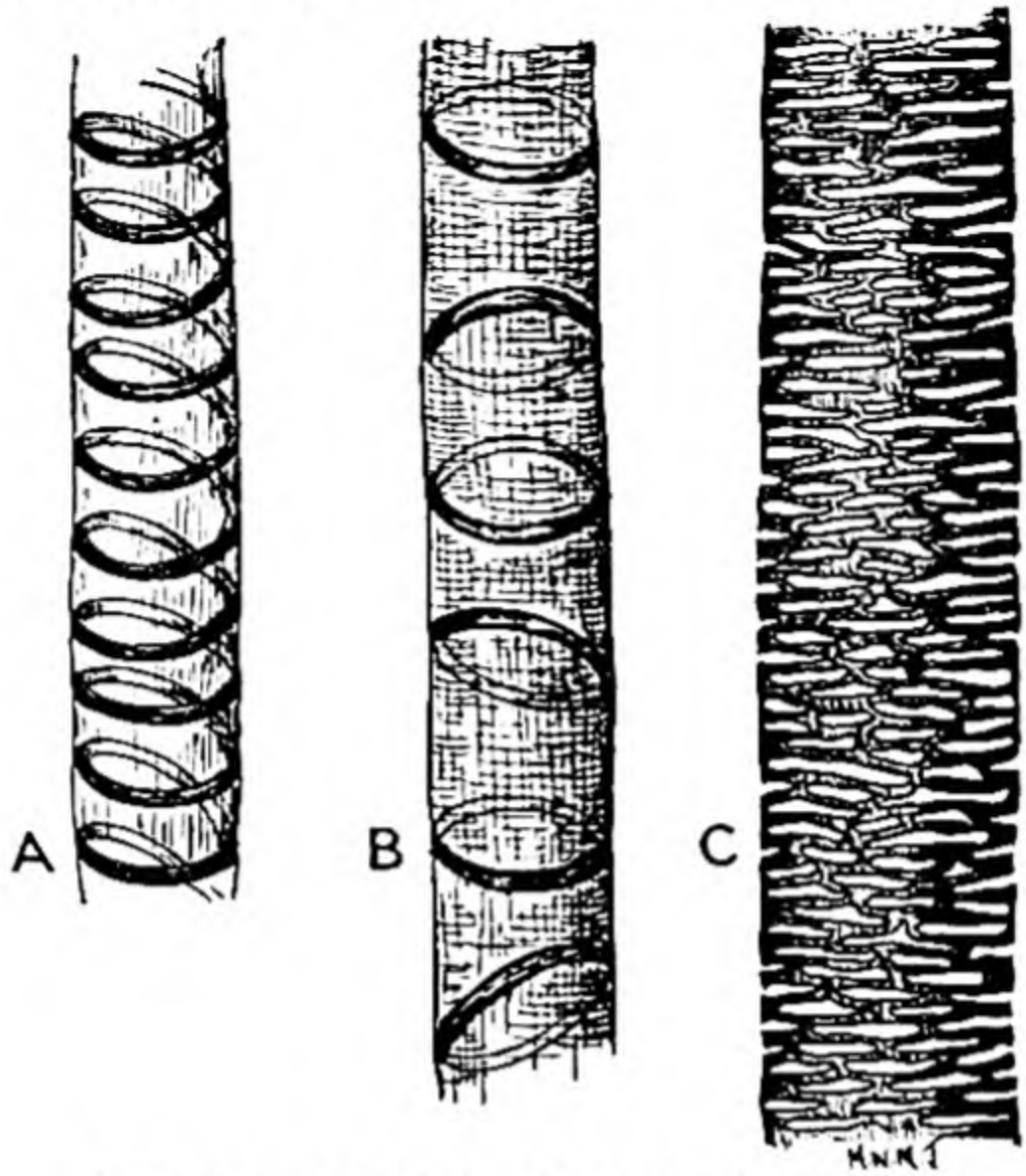


FIG. 224 – Xylem vessels, variously thickened.
A., Spiral; *B.*, Annular; *C.*, Reticulate.

page 462). For conduction of certain effects of stimulation in plants see Chapter 27.

Conducting Tissues of Plants

The conducting tissues of plants are sharply divisible into two groups, namely, those of the **xylem** and those of the **phloem**. The *vessels* of the xylem take the form of tubes, formed from vertical rows of cells by the breaking down of their transverse walls, either completely, as in the oak, or all but a rim, as in the lime, whilst in the alder a number of cross-bars remain to represent the original walls. The living contents of the vessels perish, and the component cells now become known as segments. These vessels are also of mechanical significance, for their walls become variously thickened. Thus in those constituting the protoxylem the thickening takes the form of a continuous spiral or a number of rings (*spiral* and *annular* thickening respectively), whilst in the older parts of the plant the thickening may be *reticulate*, forming an open network. This latter type is frequently found to contain a special type of pit (page 324), known as a *bordered pit*. It differs from an ordinary pit in that it is covered by a perforated dome. In two laterally adjacent vessels bordered pits usually coincide in position, so that communication is established.

The thickening of the walls enables the vessels to withstand negative pressure during active transpiration.

As well as vessels, *tracheids* occur in the xylem. Each is a single, pro-

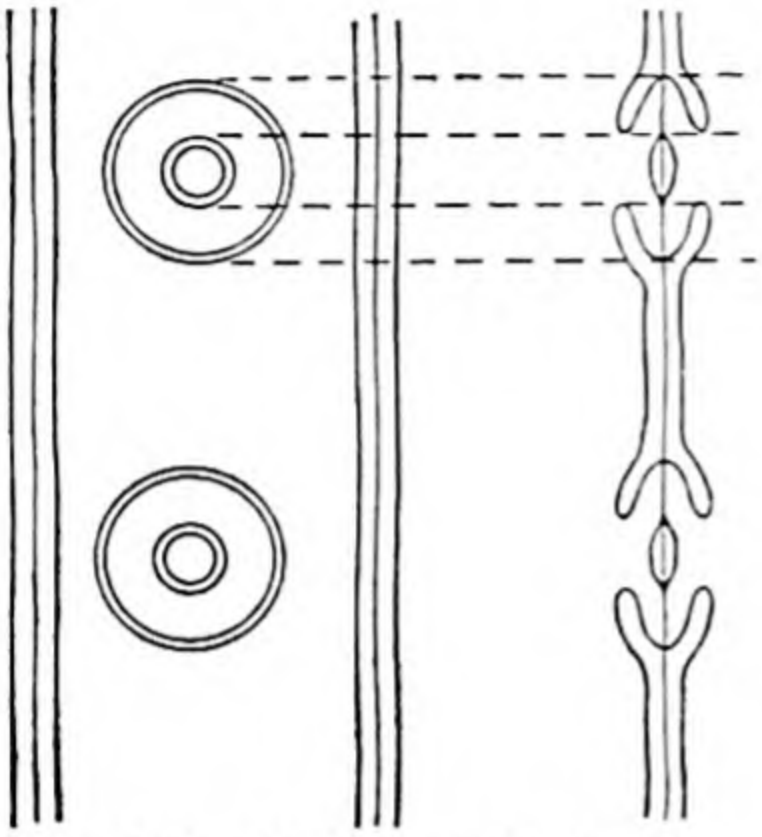


FIG. 225 – *Pinus*. Two bordered pits.

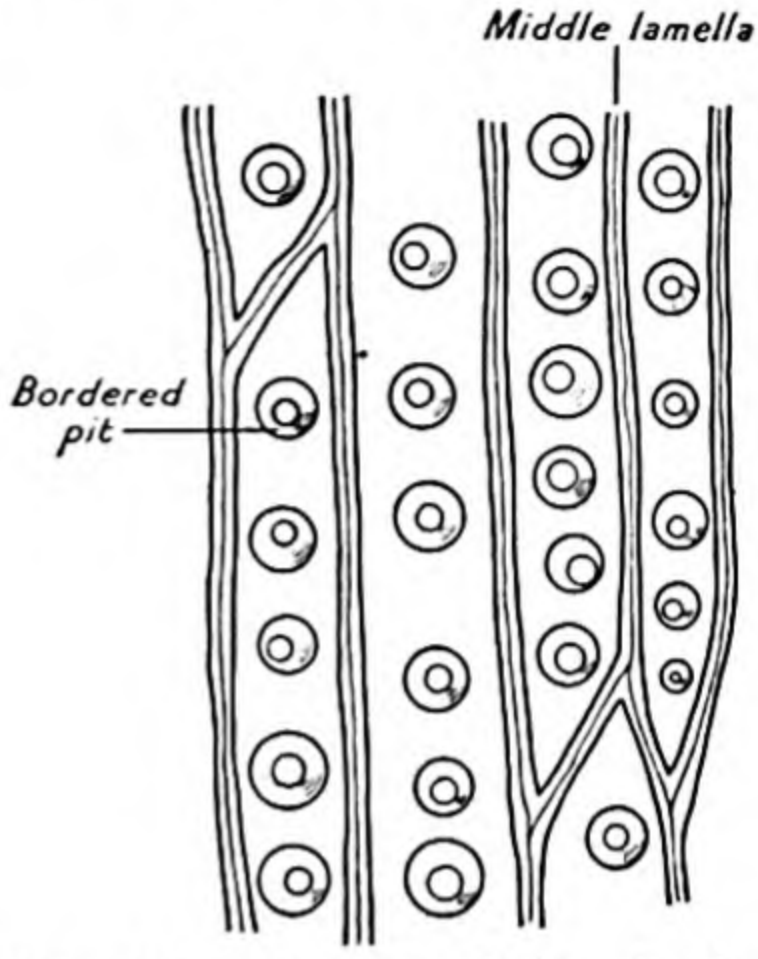


FIG. 226 – *Pinus*. Tracheids, showing bordered pits.

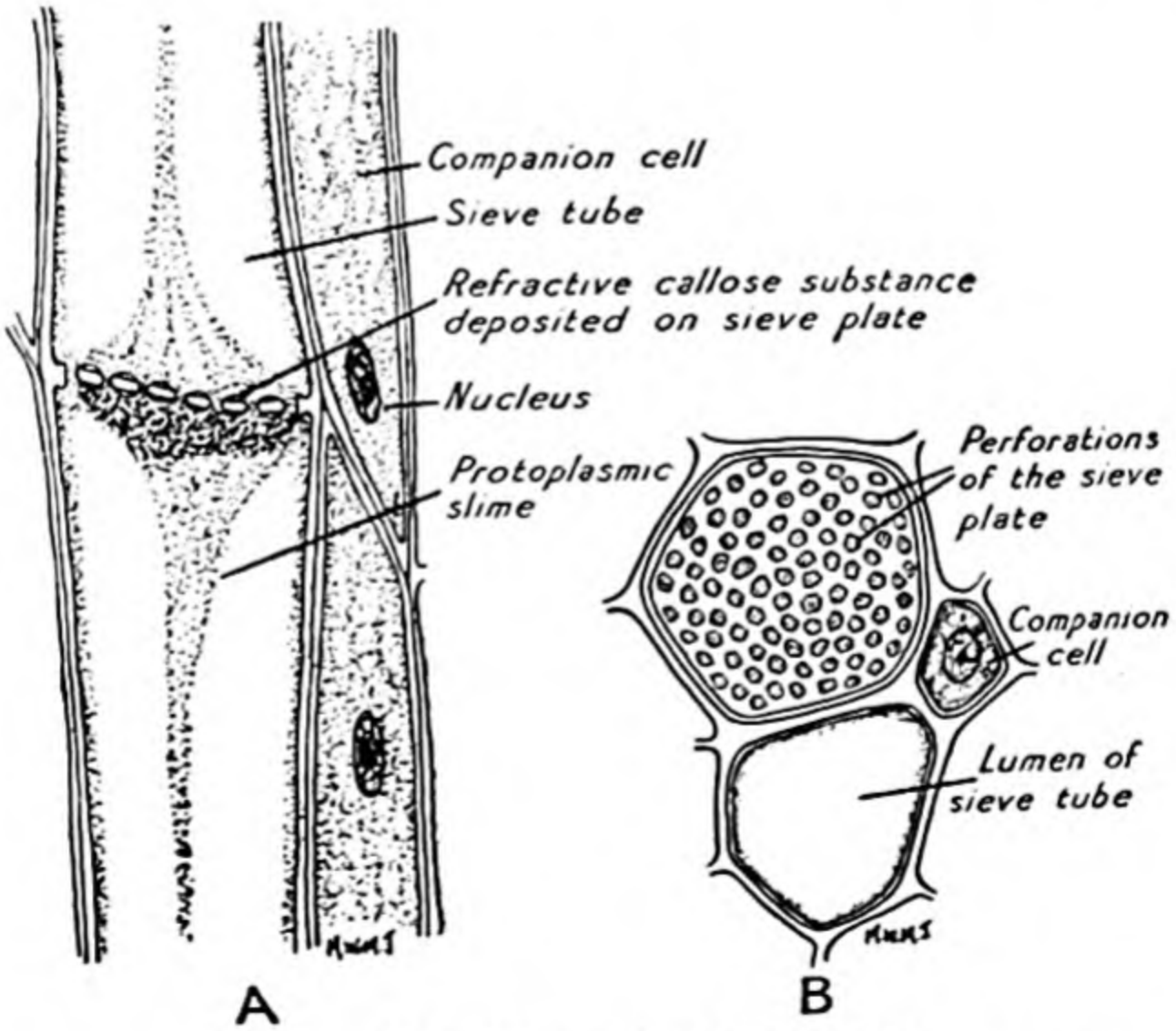


FIG. 227 – Elements of the phloem.
A., Lateral view of a sieve tube and companion cell; *B.*, Transverse section of a sieve plate.

senchymatous cell, the contents of which are dead, whilst the wall may be spirally thickened or contain bordered pits. Tracheids are more primitive than vessels, to the exclusion of which they occur in Pteridophyta and Gymnospermae, combining the functions of water-conduction and mechanical support, functions which, in most Angiospermae, are separately performed by vessels (conduction) and fibres (support).

The **phloem** is made up of structures somewhat similar to the xylem vessels and known as *sieve tubes*. Each consists of a row of cells in linear continuity, but the transverse walls separating them are densely perforated, and are not completely broken down, as they are in the formation of xylem vessels. These perforated partitions are termed **sieve plates**. Through these perforations the protoplasm of adjacent segments is continuous, for the segments, unlike those of the xylem, retain their living contents. Before development of a sieve tube segment is complete the cell divides unequally, the larger product giving rise to the segment of the sieve tube, and the smaller becoming a *companion cell*, present only in Angiospermae. The nucleus of the sieve tube segment disappears, whilst the protoplasm is confined to a narrow lining. The companion cell, on the other hand, retains its nucleus embedded in a dense mass of protoplasm. It will be apparent, therefore, that the phloem differs markedly from the xylem. Since the walls of the sieve tubes do not become lignified they are able to retain their protoplasmic lining, and thus may well be actively secretory, and not merely passive channels, as are the tracheids and vessels of the xylem. The companion cells of the phloem have no counterpart amongst the tissues of the xylem.

The types of cell occurring in the animal and plant body may be conveniently summarised in the form of a table:

Function	Animal	Plant
Mechanical	Connective tissue	Collenchyma
	Cartilage	Sclerenchyma
	Bone	Xylem vessels
	Blood	Parenchyma (cell-sap of)
Protection	Skin	Epidermis
Internal surface	Endothelium	Parenchyma
Secretion	Gland-cells	Gland-cells
Conduction of food	—	Vessels
		Tracheids
		Sieve tubes
Conduction of impulses	Nerve	—
Contraction	Muscle	—

Arteries, Veins and Capillaries

The wall of an *artery* is essentially divisible into three layers. The lining is composed of pavement endothelium, with the cells elongated in the main axis of the vessel. The middle layer is double. Next to the lining is a fenestrated membrane of yellow elastic fibres, covered by a layer of circularly disposed unstriped muscles, with more elastic fibres connected at intervals, especially in large arteries, with the fenestrated membrane. The outer coat is composed of connective tissue, mostly white, but with some yellow fibres. It is very strong and merges with the surrounding connective tissue fixing the artery in position.

Basically a *vein* is similar in structure. The endothelial cells are less elongated and the fenestrated membrane less well developed, containing much white connective tissue. Valves are constituted by folds in the endothelium and membrane.

Capillaries consist of endothelium only, continuous with that of arteries and veins. The cell-outlines are often ill-defined – e.g. in the choroid coat of the eye and in glomeruli – and the endothelium may be deficient, as in the liver (see page 342).

Mammalian Organ Histology

The association of tissues in the formation of organs assumes important proportions in higher animals, and examples of such organs will be described from the histological view-point. Description of the structure of the kidney will be reserved till page 444, where the function of that organ is considered.

INTESTINE. The wall of the small intestine is divisible into four layers. Adjacent to the lumen is a simple columnar endothelium, the cells of which play an active part in the absorption of digested food. It covers a vast number of finger-like projections, each of which is known as a **villus**. The deep recesses between neighbouring villi are the **crypts of Lieberkühn**, actively glandular and secreting enzymes. Outside this endothelium is a thick layer of areolar tissue, constituting the **submucosa**. Embedded in this are the mucus-secreting *Brunner's glands*, ducts from which discharge into the crypts. They are present only in the duodenum. Just outside the bases of the villi is a layer of involuntary muscle, termed the *muscularis mucosae*, whose activity results in the protraction and retraction of the villi, together with *Meissner's plexus* (a network of autonomic nerve fibres). The areolar tissue extends into the villi, supporting there the capillaries, lacteals and nerve-net. Surrounding the submucosa is a layer of circular muscle, followed by a layer of longitudinal muscle, the two being separated by a further nerve-net, known as *Auerbach's plexus*. Between them these two muscle layers maintain peristalsis (page 392). The whole is enclosed by the *serous coat*, consisting of areolar tissue and pavement epithelium inseparable from that of the mesentery.

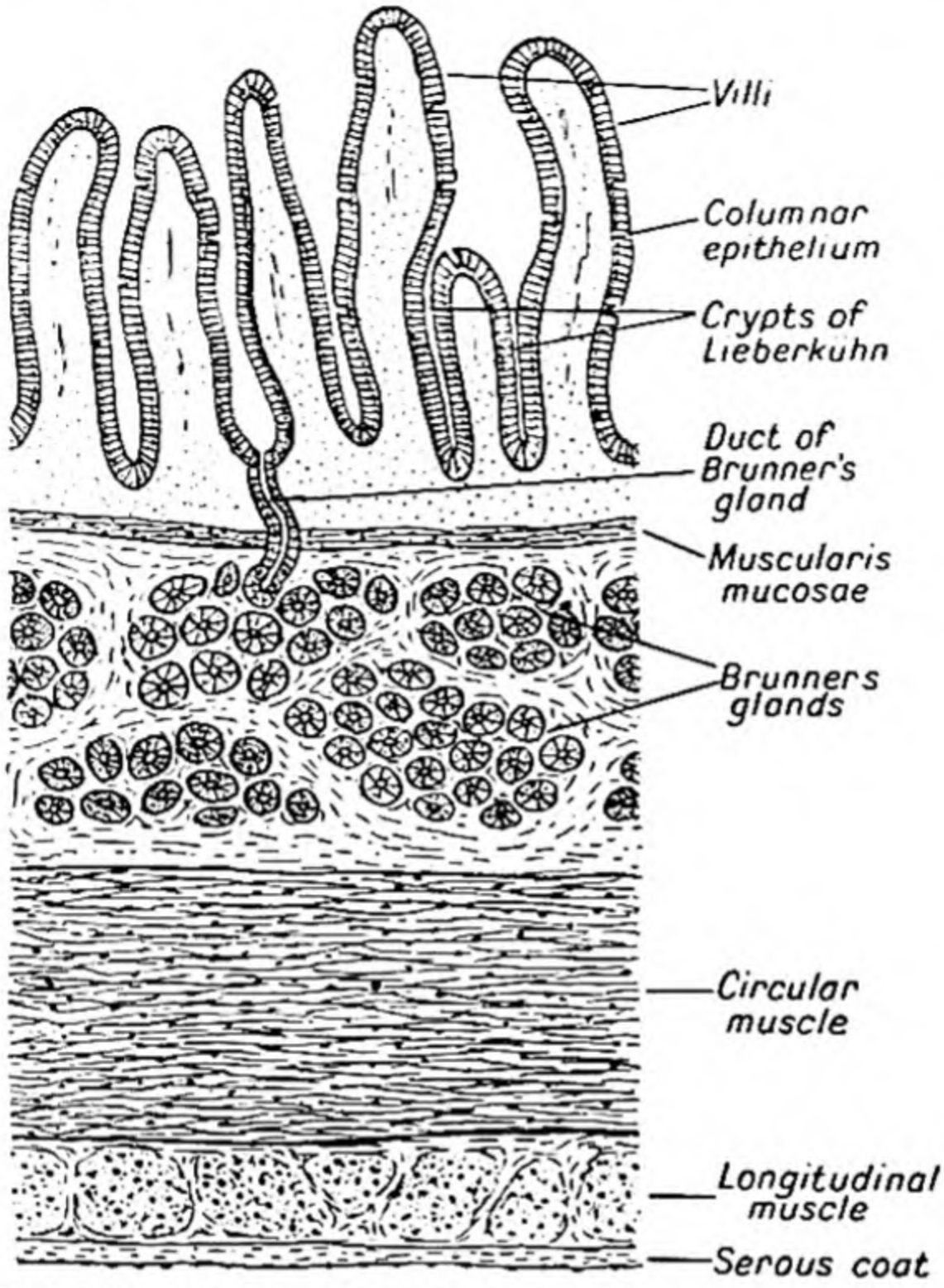


FIG. 228 – Portion of a transverse section of the intestine of a mammal.

STOMACH. This is composed of the same four layers as in the intestine, but neither villi nor Brunner's glands are present. The lining is smooth and is marked by the numerous openings of the deeply invaginated *gastric glands*, which branch occasionally at their inner extremities. *Peptic cells*, which secrete pepsin, and large *oxyntic cells* for the production of hydrochloric acid are to be found deep in the glands, whilst mucus is formed by the general endothelium lining the stomach wall and the ducts. No oxyntic cells occur at the pyloric end of the stomach.

LIVER. The liver is divided into a large number of polyhedral lobules, each about 1 mm. in diameter. Each consists of a mass of radially-arranged cells, permeated by very wide blood-capillaries, or *sinusoids*. The cells themselves are traversed by a network of *canaliculi*, and they may frequently be seen to contain granules of glycogen (see page 371).

The vessels associated with the lobules are of great importance, and are best considered under two headings.

(i) *Bile-channels.* These commence as a network between the cells, constituting the *inter-cellular bile-channels.* They all join at the periphery of each lobule, and the vessel so formed, enclosing the lobule, is

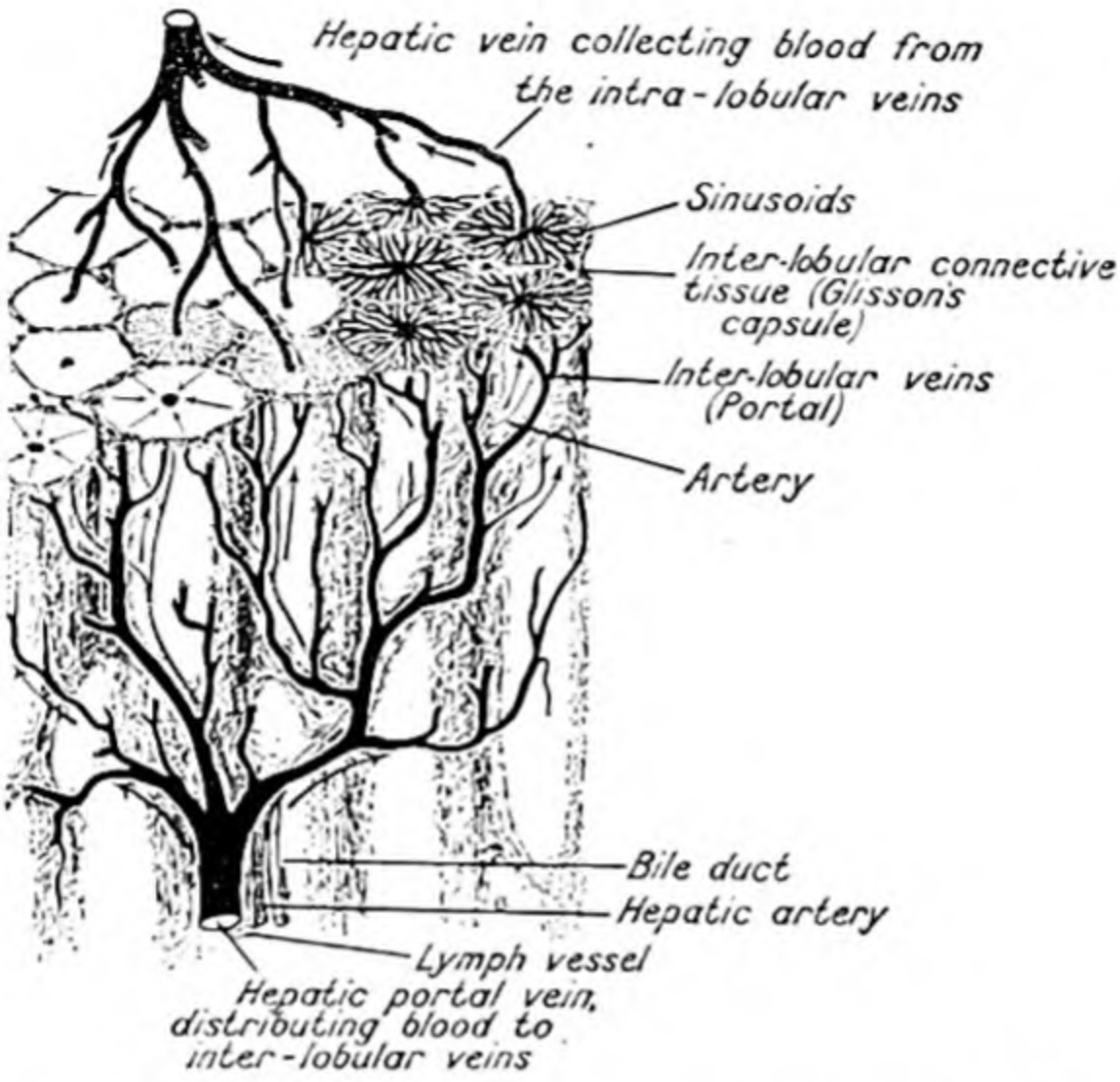


FIG. 229 – Diagram to show general structure (lobules and blood-supply) of mammalian liver.

the *inter-lobular bile-channel.* These all eventually unite to join the bile-duct.

(ii) *Blood-channels.* Here both the afferent and efferent vessels, to and from the liver respectively, must be considered. The afferent blood-supply arrives via the hepatic artery and the hepatic portal vein. Branches of them pass between the lobules as the *inter-lobular blood-channels,* being enclosed, together with the inter-lobular bile-channels, in a connective tissue sheath, much more prominent in some animals than in others and known as the *capsule of Glisson.* Branches of the two blood-vessels unite at the periphery of each lobule, and the conjoined vessels pass between the cells as the *inter-cellular blood-channels.* The efferent system is formed by the union of these branches in the centre of each lobule, where they form the *intra-lobular vein.* These all eventually unite to form the hepatic vein, which leaves the dorsal surface of the liver. Much of this rather complicated arrangement will be made clear by reference to Fig. 229.

It is worthy of note that the endothelium (lining) of the hepatic blood-capillaries is deficient, so that blood comes to lie in ill-defined spaces, or *sinusoids,* bathing the hepatic cells. Many of the residual cells of this

endothelium, known as *stellate cells* (or *cells of Kupffer*), are responsible for the destruction of the red corpuscles in the liver.

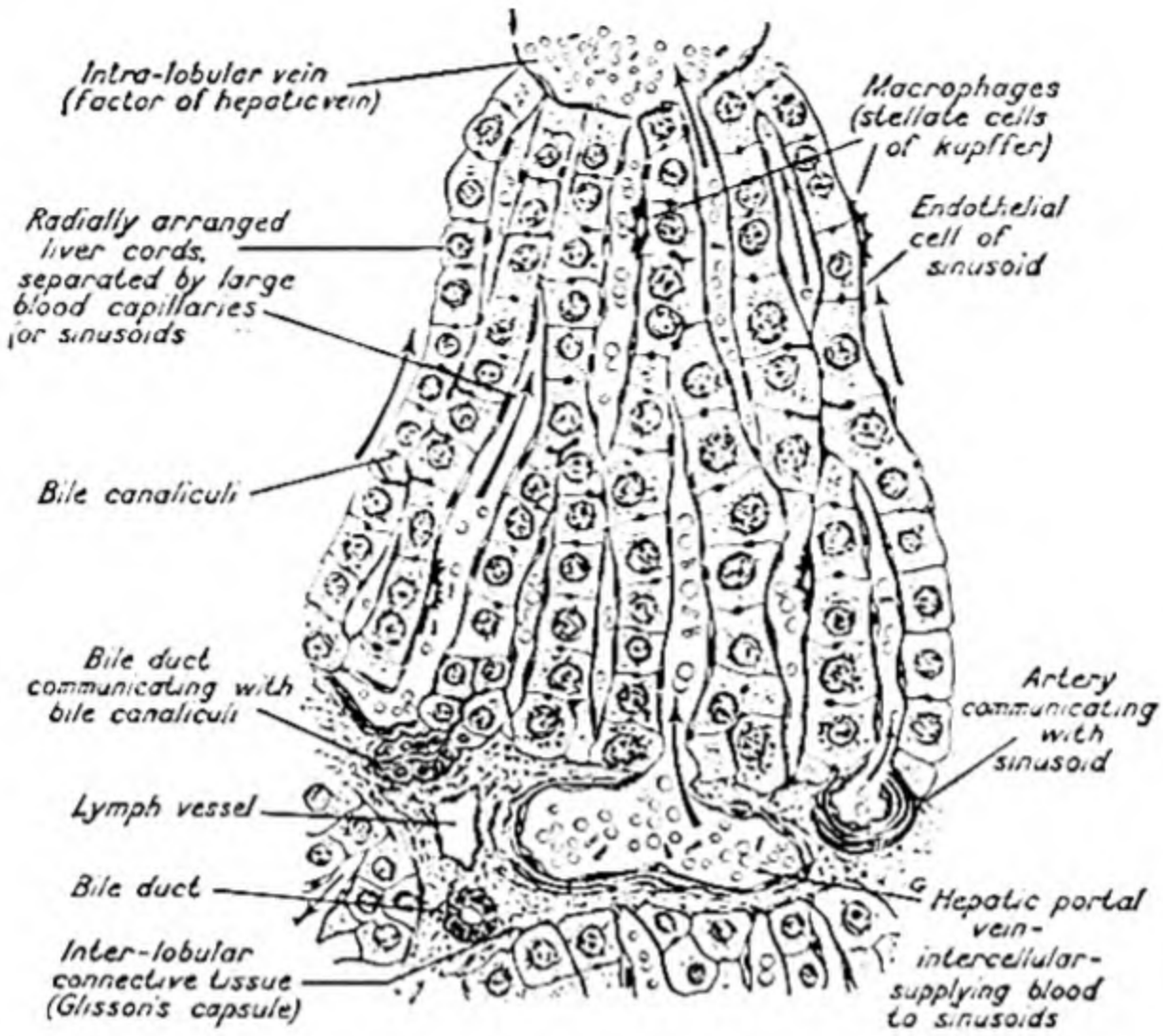

Intra-lobular vein (factor of hepatic vein)
Macrophages (stellate cells of Kupffer)
Radially arranged liver cords, separated by large blood capillaries or sinusoids
Endothelial cell of sinusoid
Bile canaliculi
Bile duct communicating with bile canaliculi
Artery communicating with sinusoid
Lymph vessel
Bile duct
Hepatic portal vein - intercellular - supplying blood to sinusoids
Inter-lobular connective tissue (Glisson's capsule)

FIG. 230 – Portion of transverse section of lobule of mammalian liver, showing the relationships between the cells and blood-sinusoids.

FUNCTIONS OF THE LIVER. Although the present chapter is devoted otherwise to the histology of tissues and organs, for the convenience of the student it is proposed here to enumerate the functions of this large and important organ, with details only of such activities as are not dealt with elsewhere.

(1) *Storage*. As a storage organ the liver is unsurpassed. The stored materials will be considered separately.

(*a*) *Glycogen*. By a complex process excess glucose from the portal blood-stream is converted into glycogen, with the assistance of the hormone insulin. The liver can also resynthesise glycogen from lactic acid, or even from pyruvic acid. When the animal is at rest some 20 % of its glycogen is stored in the liver and the remainder in the muscles. When required the glycogen is reconverted into glucose with the aid of the enzyme *glycogenase*. In shortage of supply the liver can form glucose from such non-carbohydrate sources as amino-acids.

(*b*) *Fat*. The lipoid *lecithin* is stored in the liver. The liver brings about considerable desaturation of fatty acids and consequently liver fat is much more unsaturated than that found in adipose tissue.

(*c*) *Vitamins A* and *D* are stored in the liver.

(*d*) *Iron and Copper*. These two metals, the former of which is a constituent of haemoglobin, whilst the latter is needed as a catalyst in its formation, are both stored in the liver.

(*e*) *Protein*. It has been suggested that very small amounts of protein may be stored in the liver.

(*f*) *Blood*. The minute factors of the hepatic blood-vessels can be varied in calibre and hence blood may be retained or discharged.

(2) *Synthesis*. Three substances concerned with the clotting of blood are formed in the liver. They are prothrombin, fibrinogen and antiprothrombin (see page 356). In addition, certain serum proteins, namely, albumins and globulins, are produced in the liver, whilst the synthesis of vitamin *A* from the plant pigment, carotene, also occurs there.

In addition, vitamin *B* 12, known as the anti-anaemic factor, is produced in the liver. It promotes the formation of erythroblasts in the bone marrow.

(3) *Bile* is secreted by the cells of the liver.

(4) *Erythrocytes*. In foetal life these are formed in the liver, this process occurring in man from the fourth to the eighth month of gestation. Subsequently the liver is responsible for the destruction of worn erythrocytes. Some of these are phagocytosed by the stellate cells (page 343), whilst others undergo haemolysis (swelling to bursting point as a result of endosmosis), liberating haemoglobin which is decomposed, the iron-protein portion of the molecule being split off, whilst the remainder is converted into the bile pigment *bilirubin*. The liver is assisted by the spleen in the performance of this function.

(5) *Detoxication*. Several toxic oxidation products of protein substances are converted into harmless form in the liver. Thus phenol, an oxidation derivative of the essential amino-acid, tyrosine, and indole, derived by putrefaction from tryptophane, itself believed necessary to the formation of cytochrome, are oxidised into innocuous compounds in the liver. Similarly benzoic acid is converted into hippuric acid, a function which the liver shares with the kidney. Certain hormones, including adrenalin, and anaesthetics are destroyed in the liver. Many drugs, such as chloral, menthol, morphine and aspirin, are removed by the liver as a result of combination with the glyconuric acid found there.

(6) *Protein metabolism*. Excess amino-acids and allied substances are de-aminated in the liver and subsequently converted into urea, as indicated on page 446. This is an essential preliminary to their elimination by the kidney.

(7) *Control of tissue fluids*. As already indicated above, plasma proteins are synthesised in the liver. These influence the distribution of fluid in the tissues. Thus, after prolonged starvation, a condition known as *hunger oedema* develops, characterised by the accumulation of fluid in the tissues and due to the depleted supply of these plasma proteins.

Finally, it must be emphasised how important is the liver in relation to the blood. It stands guard, as it were, over the blood arriving via the hepatic portal vein and the hepatic artery: it censors its contents before allowing distribution to the remainder of the body. Being a very large organ, its activities result in the liberation of a considerable amount of heat.

PANCREAS. This gland is subdivided into a large number of *acini*, each consisting of a ring of secretory cells surrounding a central duct, or *alveolus*, branches from which pass between the cells. Each *acinus* is embedded in connective tissue, in which occur blood-capillaries.

Arising as diverticula of the ducts of the pancreas, and subsequently losing all connexion with them, are small masses of cells, irregularly arranged, which constitutes the **islets of Langerhans**. The blood-capillaries of the islets are very large and irregular.

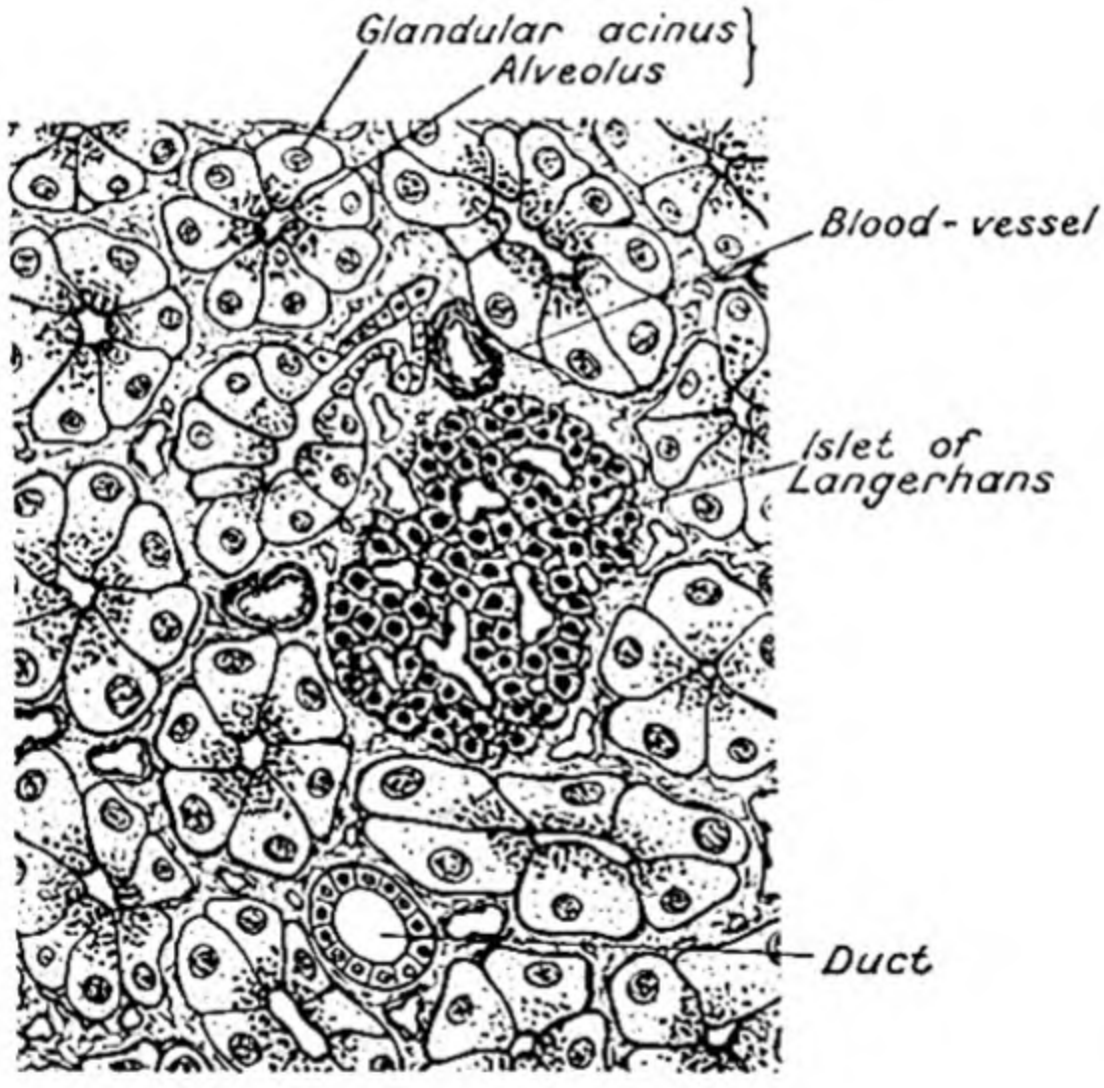


FIG. 231 – Portion of a section of mammalian pancreas.

THYROID. This important endocrine organ consists of numerous spherical vesicles, separated by connective tissue. The wall of each vesicle is composed of a single layer of cubical epithelium, whilst the cavities contain, in colloidal form, the secretion of the gland – thyroxin (see page 480). There is an abundant blood-supply, masses of capillaries surrounding the vesicles and extending between the cells.

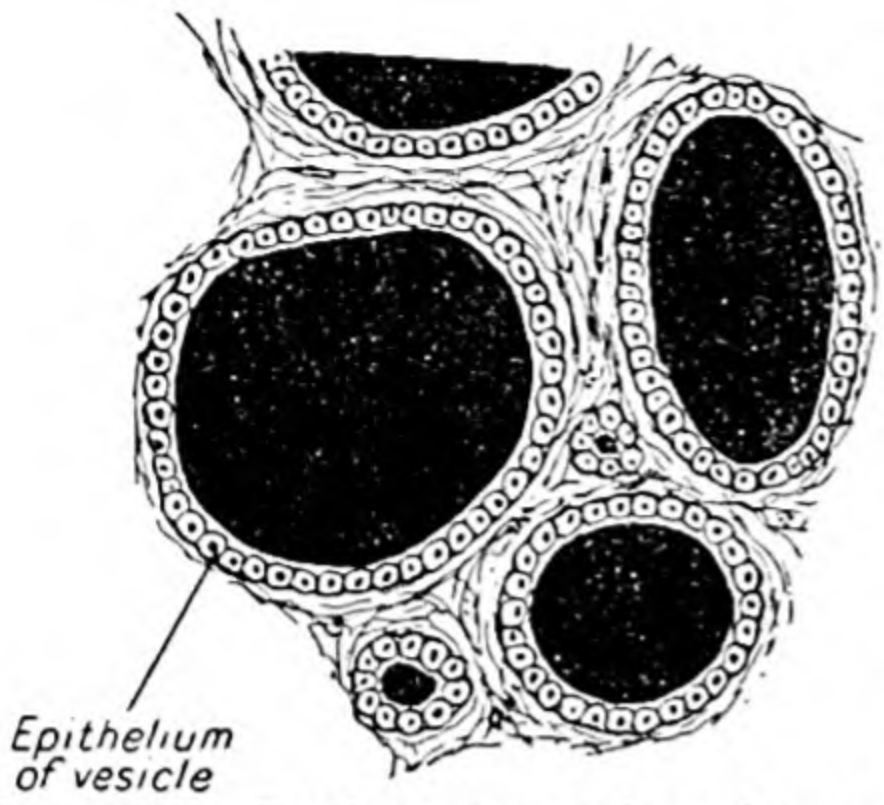


FIG. 232 – Portion of a section of mammalian thyroid gland.

OVARY. The mammalian ovary consists of a small, almost solid, mass of connective tissue, covered by germinal epithelium – the layer giving rise to the germ-cells. A little distance below the surface lies a mass of immature follicles. At first each consists of a single, large oögonium (page 319), surrounded by a single layer of flattened cells, and at this stage it is termed a *primary follicle*. The oögonium now becomes a primary oöcyte, whilst the surrounding layer of cells becomes stratified, forming a *secondary follicle*. A thick membrane, known as the *zona pellucida*, comes to enclose the oöcyte, which undergoes the next maturation division to form a secondary oöcyte. Meanwhile small pools of follicular fluid appear amongst the covering cells and these pools pass into the centre and coalesce to envelop the oöcyte, which is now stationed at the apex of a small mound of cells. The structure of such a mature *Graafian follicle* is shown in Fig. 233. As the follicle matures it moves to the surface of the ovary and at ovulation

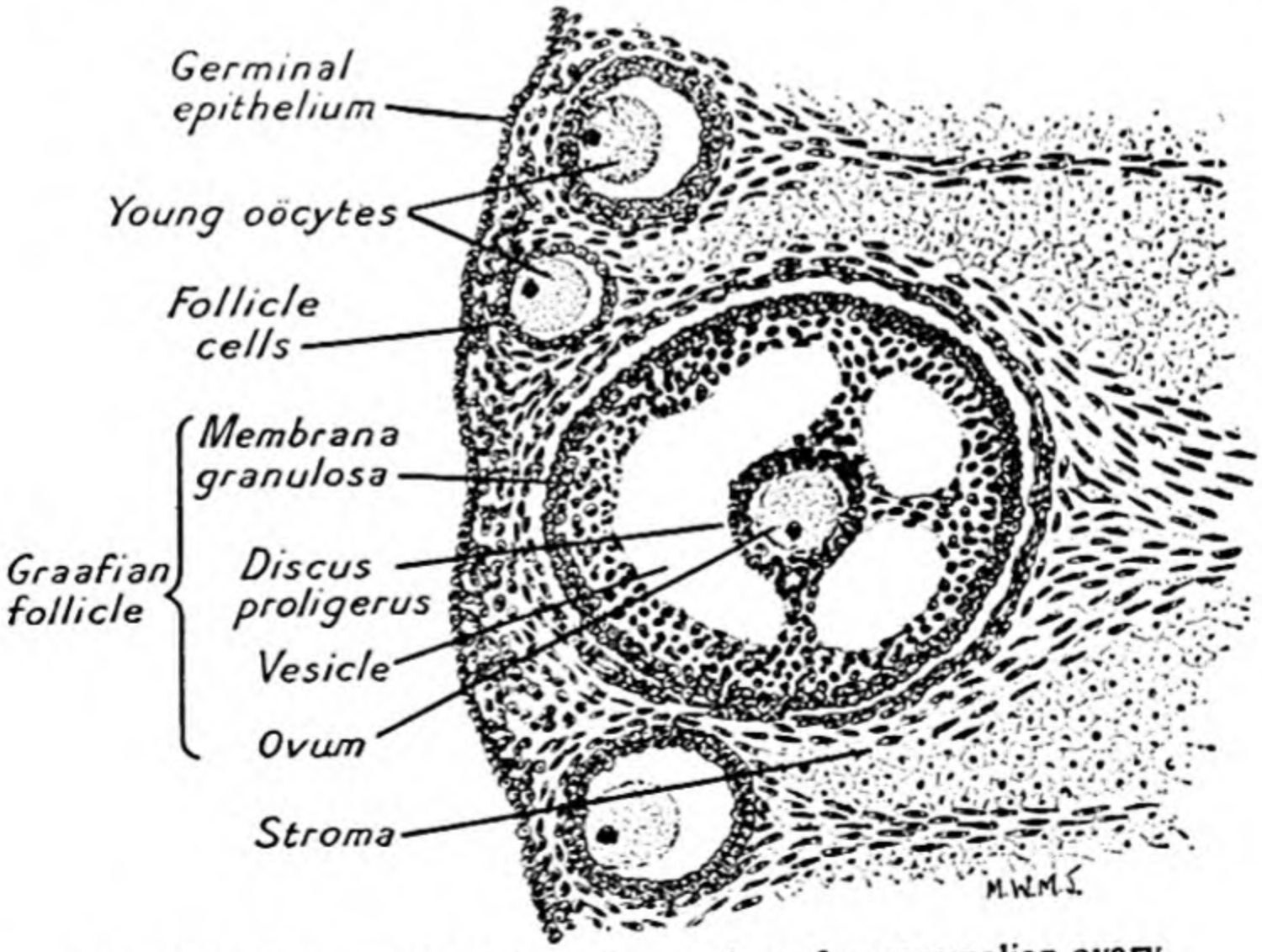


FIG. 233 – Transverse section of a portion of a mammalian ovary.

the secondary oöcyte is discharged. Upon fertilisation, maturation is completed by the extrusion of a second polar body (page 320) and a zygote is formed. Some of the cells of the ovary are glandular, secreting sex hormones (page 487).

CORPUS LUTEUM. After the extrusion of the secondary oöcyte the follicle collapses and a blood-clot, mixed with residual follicular fluid, remains in the centre. The follicular cells enlarge considerably and become vacuolated. Within them accumulates a yellow pigment to such an extent as to impart the characteristic colour to the whole body – hence its name

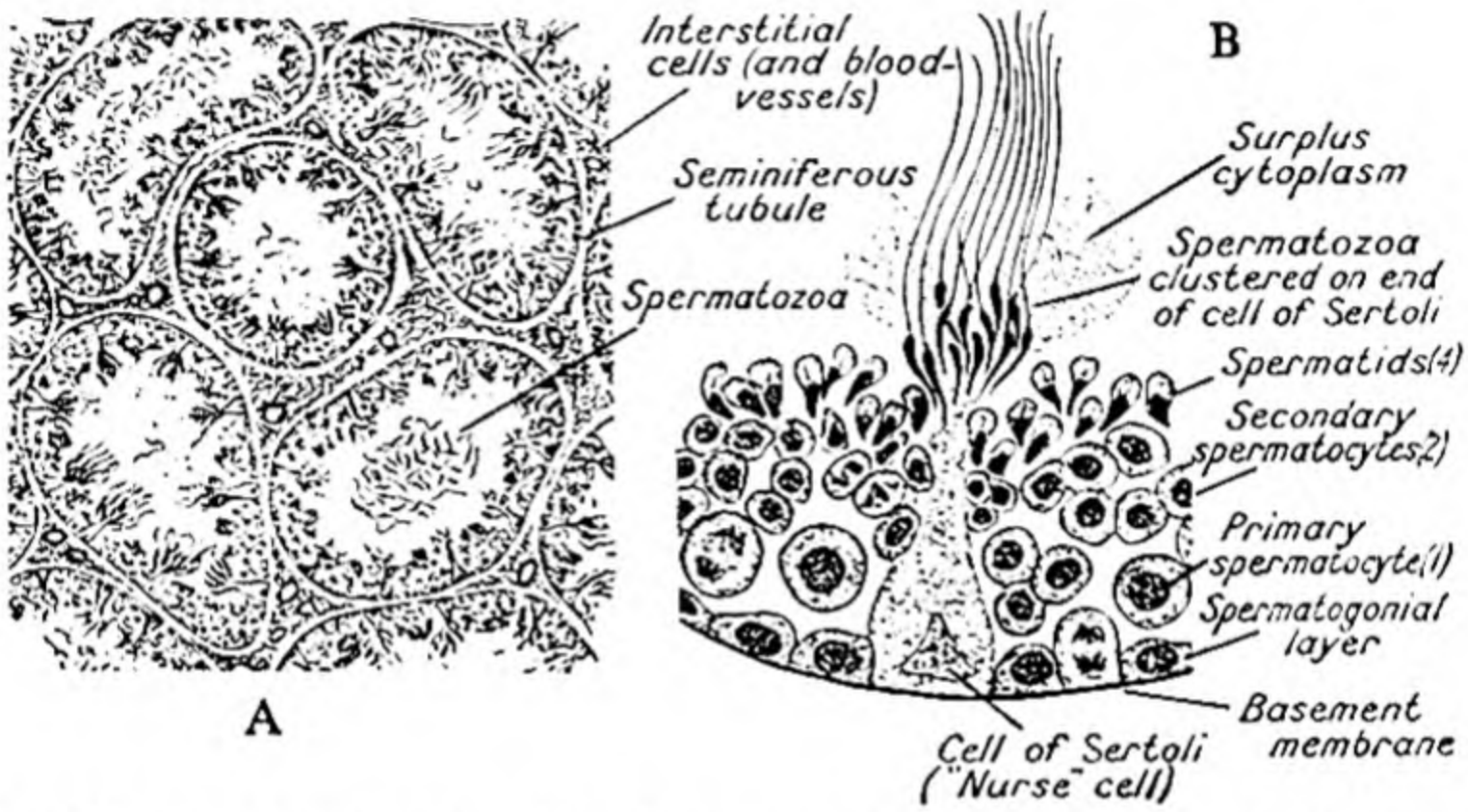


FIG. 234 – *A.*, Transverse section of a portion of a mammalian testis. *B.*, A high power enlargement of part of one seminiferous tubule, showing germinal epithelium.

(corpus luteum = the yellow body). These are termed *lutein cells*. As development proceeds, capillaries ramify amongst the lutein cells, thus giving typical endocrine structure to the organ. Finally, fibroblasts lay down a capsule of connective tissue around the fluid and clotted blood in the centre. Should fertilisation not occur the corpus luteum soon shows signs of regression and eventually becomes a small, white scar, known as the *corpus albicans*. The significance of the corpus luteum is discussed on page 488).

TESTIS. This organ is imperfectly subdivided by strands of connective tissue into lobules, consisting of *seminiferous tubules*. These are of considerable length and at first much convoluted. Near the posterior end of the testis the tubules straighten out to form composite ducts, constituting the *rete testis*, and these eventually convey spermatozoa to the epididymis (page 174). Each seminiferous tubule is composed of several layers. Outermost is the *basement membrane*, and within are represented the various stages in the development of mature spermatozoa, as shown in Fig 234. Interspersed with the reproductive cells are interstitial cells (to

secrete male hormones) and supporting cells. These latter enlarge and their nuclei become polymorphic. In this condition they are known as the *cells of Sertoli* and are believed to be concerned with the nourishment of developing spermatozoa. The testis is enclosed within a fibrous sheath, termed the *tunica albuginea*.

A spermatozoön itself is a highly specialised cell whose structure, though variable in detail, is basically similar throughout the vertebrates. In the following description and in Fig. 325 that of the bull will be taken as reasonably representative.

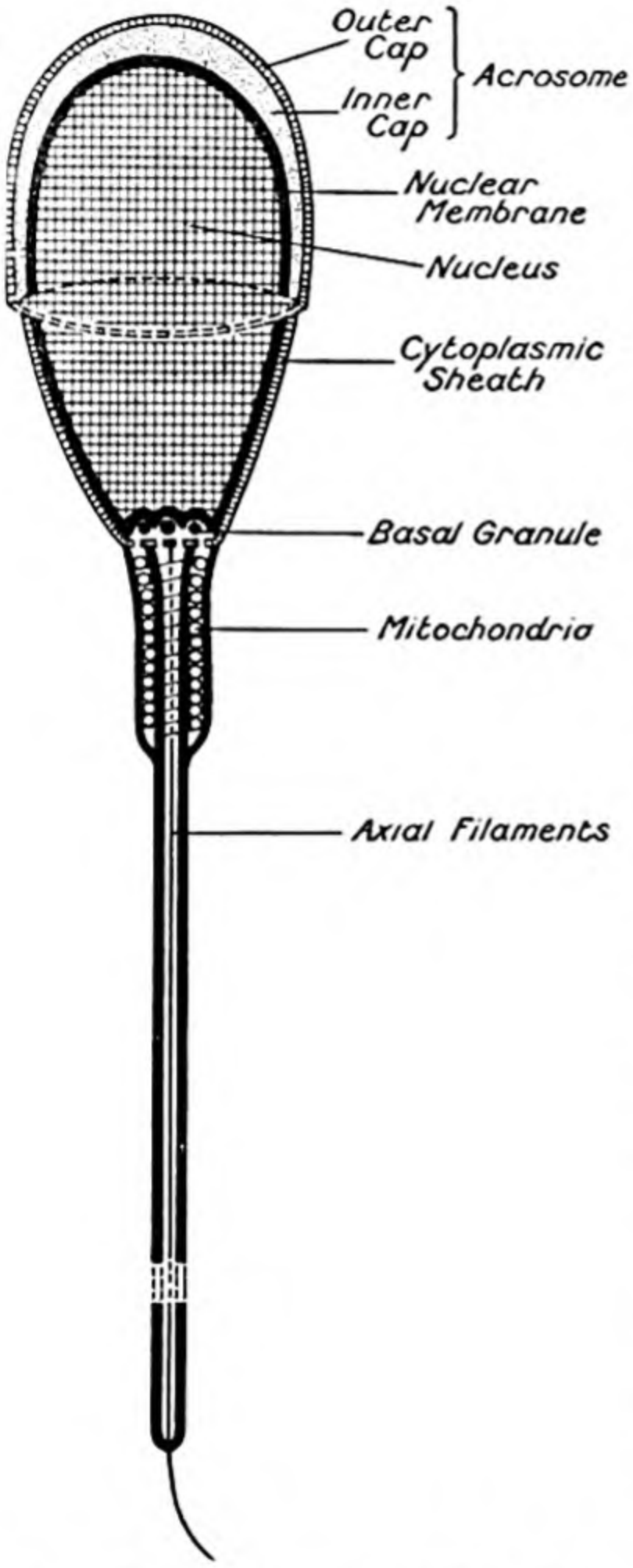


FIG. 235 – Diagram of a mammalian Spermatozoön (bull). (The head and mid-piece after Bishop and Austin.)

HEAD. The nucleus consists of densely packed chromatin. In the bull about 43% is composed of desoxyribonucleic acid (*DNA*) and the remaining 57% of protein. It is interesting to note that the *DNA* is about half that found in somatic cells, indicating that genetic properties are somehow related to the structure of the *DNA* molecules. The leading half of the nucleus is covered by a two-layered cap – the *acrosome*. The idea that this assists mechanically in the penetration of the egg at fertilisation is now largely discredited and its possible function is referred to on page 562. The posterior half of the nucleus is enclosed within a cytoplasmic sheath, continuous with the acrosome.

TAIL. This is relatively long (up to 250μ) and divisible into four regions – neck, mid-piece, main-piece and end-piece. It arises from the spermatid centrioles. Embedded in the nucleus and attached to the short neck are two (or three) basal granules. An axial core runs from the neck throughout the tail and is composed of twenty discrete, straight

fibres, arranged with two central fibres surrounded by two rings of nine each. The mid-piece consists of a double mitochondrial spiral surrounding the axial core. In the main-piece the axial core is surrounded by a tough protein sheath, with a slender 'rib' down either side, whilst the end-piece is very short and there is no covering sheath.

An important property of the sperm is its motility. It is possible that the nine fibres of the outer ring are contractile, whilst the others conduct rhythmical impulses from the neck. The mid-piece is probably the power-house, utilising enzymes derived from the mitochondria. Spermatozoa remain quiescent in the epididymis but become activated, possibly by exposure to a high concentration of oxygen, on release. Passage of spermatozoa from vagina to oviduct is largely facilitated by muscular contraction and ciliary currents in the wall of the female genital tract, rather than by their own powers of locomotion, which assist only in the penetration of the egg.

Further reading on this topic may be found in an article by M. W. H. Bishop and C. R. Austin in *Endeavour*, Vol. XVI, Number 63 (I.C.I.), from which article the author derived most of his up-to-date information.

PENIS. This organ, through which runs the urethra, is characterised by the possession of three bands of erectile tissue. The most posterior band is the *corpus spongiosum*, surrounding the urethra, whilst anterior to this are the paired *corpora cavernosa* (page 680). In conditions of sexual stimulation these become gorged with blood. This is achieved by the contraction of the unusually muscular walls of the veins which drain the penis, thus temporarily preventing the return of the blood to circulation.

PRACTICAL WORK

Plant Tissues

Examine transverse and longitudinal sections of the following plant organs with a view to discovering their tissue-components. Stain them with the reagents indicated, and mount in glycerol.

(A) PARENCHYMA. Cortex of stem of *Cucurbita*. Stain with methylene blue (this stains all cellulose walls).

(B) COLLENCHYMA. Mid-rib of a young leaf. Superficial layers beneath the epidermis of the stem of *Cucurbita*. Stain with Schultz's solution (chlor-zinc-iodide) which turns cellulose blue, or haematoxylin, which stains it purple.

(C) SCLERENCHYMA. Leaf of *Pinus*. Stem of *Cucurbita*, within the collenchymatous layer. Stain with aniline sulphate (yellow), and phloroglucin followed by concentrated hydrochloric acid (red).

(D) XYLEM. Stem of *Cucurbita*. Here longitudinal sections are as important as transverse. Examine the stem of *Pinus* for tracheids. Stain as for sclerenchyma.

(E) PHLOEM. Stem of *Cucurbita*. Look for sieve plates.
(F) PITS. Stem of *Pinus*, especially in longitudinal section.
(G) CYSTOLITHS. Leaf of stinging nettle (*Urtica*).

Plant cells may be isolated and examined individually by treatment of selected plant organs in various ways, resulting in their disintegration and the liberation of separate cells. Such a process is termed **maceration**, for which several techniques are available.

For a herbaceous or woody stem Schultze fluid may be employed. A small piece of stem is cut into radial or tangential longitudinal sections, which are placed in a test-tube. A few crystals of potassium chlorate are added, followed by a little concentrated nitric acid. The mixture is heated until fumes cease to be evolved, when, after cooling, water is added and the contents of the tube poured on to a filter-paper, where they are washed with water. A portion of the macerated tissue is now transferred to a slide bearing a drop of glycerol, where the tissue is teased out and covered for microscopic examination.

Isolation of the cellular components of a herbaceous stem may also be effected if similar sections are placed in a mixture of three parts alcohol and one part concentrated hydrochloric acid for twenty-four hours. They are then rinsed with water and treated for a short time with 10% caustic potash solution. The tissues are now easily disintegrated by pressure of the cover-glass, glycerol being again employed as the mounting medium.

Privet or other similar leaves may be subjected to a different treatment. They are boiled in 10% caustic potash solution for about ten minutes, after which they are washed in water and short marginal strips cut off under water with scissors. After sufficient boiling the strips will readily disintegrate into three layers – upper epidermis, mesophyll and lower epidermis – which can be mounted separately in glycerol, the mesophyll requiring to be either teased or crushed beneath the cover-glass.

Animal Tissues

Examine prepared section of connective tissue, cartilage, bone, muscles, nerves and glands.

BLOOD. Clean two slides in acid alcohol, and at one end of one of them place a small drop of frog's blood.[1] Draw the other slide across the one bearing the blood, holding it at an angle of about 45°, pressing lightly so that the blood is distributed to form a thin smear. Carefully dry the slide over a very low Bunsen flame. Put on to the slide a few drops of Leishmann's stain and rock to and fro until the whole is covered. Leave for one minute. Add double the number of drops of distilled water and again rock to form a homogenous mixture of stain and water. After fifteen minutes rinse the slide in distilled water and dry with blotting

[1] Frog's blood is preferable, owing to the larger size of the erythrocytes and the fact that they contain nuclei.

paper. Examine direct under oil-immersion. The erythrocytes are pink, whilst the nuclei of the leucocytes are blue-purple. Parasites in the blood have their nuclei stained red and their cytoplasm blue.

Make a second smear as before, and place the slide in absolute alcohol for five minutes. Take 10 drops of Giemsa (methylene-blue-eosin) in a clock-glass and add 10 c.c. of distilled water, mixing well. Immerse the slide in this solution for about twenty minutes. Wash off superfluous stain with distilled water and dry with blotting paper. Erythrocytes are now mauve, parasites blue and leucocytes reddish-violet.

CHAPTER 21

Division of Labour in Animals and Plants

It is apparent from the two preceding chapters that the development of a cellular organism is based upon two processes, namely, cell-division and differentiation. A Protozoön is a complete, non-cellular organism; it is an individual. When cell-division occurs the two component halves separate, each becoming adult. The same is true of the non-cellular Algae – e.g., *Chlamydomonas*. But it is possible for division to occur and the daughter-cells thus formed to remain in anatomical, and possibly physiological, continuity. This may take one or two forms. Either all the cells may remain identical, each one capable of effecting each and all of its own life-processes, or else various cells may become specialised to the exclusive performance of certain functions. This introduces the phenomenon of interdependence between the component cells, for specialisation in one direction has involved the loss of powers over other functions. Thus the aggregate of cells functions as one collective whole.

Colonies of Cells

In the instance referred to above, where a number of similar cells become associated a **colony** is said to have been formed. Thus a single filament of *Spirogyra* is essentially a colony, since no form of interdependence is exhibited between the constituent cells. But colony-formation amongst the Algae becomes very much more highly organised than this, so much so that there is no clear line of demarcation between colonial forms and true cellular plants. Thus *Pandorina* consists of a mass of 16 cells, embedded in a mucilaginous sphere. Each cell essentially resembles *Chlamydomonas* in structure, and locomotion is effected by the combined beating of the flagella, which project from the surface of the colony. Each cell is capable of both vegetative and reproductive functions, sexual and asexual. There is, in fact, no semblance of specialisation of function amongst them, though the beat of the flagella must be co-ordinated in some way to bring about locomotion of the whole colony.

A slight advance on this condition is shown by *Eudorina*. This, too, is a spherical colony, consisting of 32 chlamydomonad cells, embedded in the surface of a hollow, mucilaginous sphere, from the cavity of which a small pore leads to the exterior. All the cells are again capable of both vegetative and reproductive functions, but *Eudorina* resembles more

advanced types of colony in the disposition of its constituent cells and in the fact that the cells are in continuity by protoplasmic processes.

There are two species of *Pleodorina*, which exhibit characters intermediate between those of *Eudorina* and the relatively advanced *Volvox*. The colonies of both species essentially resemble that of *Eudorina*, but in *P. illinoiensis* there are 32 cells, four of which are smaller than the remainder, from which they further differ in that their function is purely vegetative. Thus they represent a plant **soma**, or body, and they die when new colonies are formed. In *P. californica* there are 64 or 128 cells, of which upwards of one-third constitute the soma, being grouped together to one side.

The series is completed by *Volvox*, already described in detail on page 185. Of the very large number of cells comprising the colony, only about 1% retain powers of division, the remainder being purely somatic. Furthermore, though the details are not finally determined, it appears that the colonies cannot each give rise to all the types of reproductive cell, sexual and asexual.

Finally, in *Fucus*, for example, the cells comprising the soma itself are not all of the same type (see below and page 193).

Cellular Structure

At this point it will be well to examine the composition of animals and plants whose bodies are made up of a number of cells, similar or differentiated. Such an organism may be described either as **cellular** or as **multi-cellular**, whilst a Protozoön or corresponding Alga may be said to be **non-cellular** or **uni-cellular**. It must now be considered which of these alternative adjectives most truly represents the relation between component cells and the body as a whole. The statement that the body of a living organism is *made up of* a number of cells implies that a certain degree of individuality is exhibited by the component cells. To what extent is this true? As has already been indicated it may perhaps be applied to such colonial organisms as *Eudorina* and *Volvox*. But where cellular differentiation has occurred it follows essentially that such individuality has been replaced by mutual interdependence. Thus the organism as a whole becomes the individual, and not the component cells. It seems more expressive, therefore, to describe a colony of cells as a multi-cellular organism, whilst an animal or plant exhibiting cellular differentiation is better referred to as cellular, implying that it is *divided up into* cells, rather than made up of them. Similarly, where such division into cells has not been effected – e.g., *Amoeba* and *Chlamydomonas* – such an organism is better described as non-cellular than as uni-cellular, since it emphasises the absence of division into cells.

Differentiation

In Chapter 20 the differentiation of the cells of higher animals and

plants was studied. In these forms specialisation has been developed to a high degree of perfection, but in some of the lowlier members of the animal- and plant-kingdoms it is demonstrated more simply. *Hydra* may be considered as an example. The structure of this animal has already been considered in Chapter 2. It remains here merely to recapitulate its principal features in so far as they relate to the problem of differentiation. The musculo-epithelial cells of the ectoderm afford a surface layer, whilst their expanded bases facilitate longitudinal contraction. The interstitial cells of the ectoderm show but little differentiation and consequently, as is the case throughout the remainder of the animal-kingdom, such unspecialised cells are the source of germ-cells. The nematoblasts show very considerable specialisation, being adapted for the extrusion of delicate threads concerned with the capture of food. Nerve-cells in the gelatinous mesogloea are specialised for the conduction of nervous impulses. In the cells of the endoderm there is markedly less visible structural specialisation. At their ends bordering the coelenteron they are considerably subdivided, effecting the ingestion of small food particles. But within them are numerous food vacuoles, since the endoderm cells are the seat of the digestive process. Their differentiation appears therefore to be physiological, but this must be accepted as an index of internal structural specialisation. As is always the case, differentiation is here accompanied by the loss of powers of individual existence. Through their mutual interdependence they accommodate the life-process of the organism, considered as a collective whole.

Fucus represents a grade of organisation amongst plants comparable with that of *Hydra* in the animal kingdom. Cellular differentiation in *Fucus* has already been described (page 193), and it will be remembered how the cells of various regions of the thallus become modified to perform certain functions, though the extent of such differentiation is much below that found in higher plants. As previously stated (page 196) the ultimate fate of each product of division of cells at the apical growing point is determined largely by its physico-chemical environment.

There is present in the majority of animals, and especially well developed in the Craniata, one tissue which takes part in a variety of processes, its component parts being separately adapted to their respective functions. This fluid is the blood, and for convenience a summary of the functions of this fluid tissue will be given here, but the majority of them are discussed in more detail elsewhere, when the separate processes are under consideration.

Functions of the Blood

The function of the blood as means of transport for dissolved substances must involve the passage of such substances into and out of the blood. This is possible only in the capillaries (page 340), and it must be clearly understood that diffusion through the walls of the capillaries is

possible to most dissolved substances, but the corpuscles are essentially retained within a closed system of tubes. The direction of diffusion – i.e. into or out of the blood – depends generally upon where the greater concentration of the given substance exists.

(I) CARRIAGE OF DISSOLVED FOOD. As the blood circulates in the capillaries of the villi (page 393) the products of digestion will diffuse into the blood through the capillary walls for transport to other parts of the body. In the tissues the plasma, or lymph, will exude through the walls of the capillaries to nourish the living cells. The diffusion of food substances into or out of the blood cannot be effected by simple physical diffusion alone, since the concentration of glucose, for example, is higher in the blood than in the intestine. Certain vital activities must contribute to the passage in the required direction.

(II) REMOVAL OF SOLUBLE WASTE MATTER. In a similar manner dissolved waste matter (excluding carbon dioxide for the moment) will pass into the blood. It will generally be conveyed first to the liver, and ultimately to the kidneys for elimination.

(III) CARRIAGE OF HORMONES. In the same way these products of secretion of the endocrine organs will be absorbed and distributed.

(IV) CARRIAGE OF OXYGEN. This function is described in more detail on page 434. It is sufficient here to notice that the diffusion of oxygen into the blood is accelerated by the presence of the haemoglobin in the red blood-corpuscles, since this substance combines loosely with the oxygen, so removing it from the sphere of action.

(V) CARRIAGE OF CARBON DIOXIDE. This function will be dealt with here at some length, and the following account of the process is based upon the description given in Yapp's *Animal Physiology*. Carbon dioxide, generated as a result of respiration (combustion) in the living tissues, diffuses into the plasma, where it combines to some extent with the water, forming carbonic acid.

$$CO_2 + H_2O \rightleftharpoons H_2CO_3$$

The reaction is catalysed by the enzyme *carbonic anhydrase*. Carbonic acid is also formed within the red corpuscles in a similar manner, when it proceeds to act with the haemoglobin, most of which is present as the potassium salt, according to the equation –

$$KHb + H_2CO_3 \rightleftharpoons KHCO_3 + HHb$$

At this stage there are therefore present the following ions –

In the plasma – $Na^{\bullet}$ and Cl'
In the corpuscles – $K^{\bullet}$, HCO_3', $H^{\bullet}$ and Hb'.

Now the walls of the corpuscles are permeable only to the smaller anions, and not at all to cations. In consequence there is a tendency for chloride ions to pass into the corpuscles and bicarbonate ions to diffuse out, and

this condition is termed a Donnan equilibrium. The greater part of the carbon dioxide is therefore virtually carried in the plasma as sodium bicarbonate. When the pressure of carbon dioxide is reduced – i.e. in the lungs – the reaction is reversed. The acidic haemoglobin, and more especially the oxy-haemoglobin, dissociate the bicarbonate, and the liberated carbon dioxide escapes from the blood.

In addition to the above, the following subsidiary methods employed in the transport of carbon dioxide should be noted.

(i) The carbon dioxide combines directly with haemoglobin, this method accounting for about 30% of the total carried. Thus –

$$HbNH_2 + CO_2 \rightleftharpoons HbNHCOOH$$

(ii) Carbonic acid combines with the sodium salts of the proteins present in the plasma. Thus –

$$NaPr + H_2CO_3 \rightleftharpoons NaHCO_3 + HPr$$

(iii) It reacts similarly with potassium phosphate. Thus –

$$K_2HPO_4 + H_2CO_3 \rightleftharpoons KHCO_3 + KH_2PO_4$$

About 5% of the carbon dioxide is carried by a combination of methods (ii) and (iii). In the lungs the reactions are, of course, reversed and the liberated carbon dioxide escapes.

(VI) CLOTTING. This is initiated by the combined activities of three substances, which are set free from the blood and adjacent tissues at any rough or damaged surface. The substances are –

(i) A substance liberated by the platelets.

(ii) *Anti-haemophilic globulin* (*AHG*), a protein present in the plasma.

(iii) *Plasma thromboplastin component* (*PTC*), also present in the plasma.

PTC first becomes activated and reacts with *AHG* to form an intermediate compound. In the presence of calcium ions this compound reacts with the substance liberated by the platelets to form *thromboplastin* (or *thrombokinase*). This compound becomes enzymically activated to convert a further plasma substance, *prothrombin*, into *thrombin*. As long as the blood is properly contained within uninjured vessels this reaction does not normally occur, in spite of the presence of a little thrombin, for it is inhibited by a further substance, *antiprothrombin* (or *heparin*), formed in the liver. As rapidly as thrombin is formed at a wound it reacts with a further protein, *fibrinogen*, present in the plasma in sol state, causing the precipitation of a dense, fibrous mass of **fibrin**, the basis of the clot. Within its interstices many corpuscles are trapped and eventually the whole dies to form the characteristic scab, beneath which the true process of healing takes place. The watery liquid, consisting of blood plasma with the clotting components no longer present, which seeps through the newly formed clot, is known as the **serum**. In order to

accelerate the process of clotting, some of the thrombin formed acts on an accelerating agent (*proaccelerin*), which in turn greatly speeds up the formation of more thrombin from prothrombin.

Haemophilia, a disease characterised by the failure of the blood to clot properly, is due to the absence of at least one of the agents involved in the long sequence of actions necessary. In most cases it is *AHG* or *PTC* which is missing. That such variations of cause occur is evident from the fact that the injection of the blood of one haemophiliac into the bloodstream of another will often impart to the blood of the latter normal powers of clotting. In such a case different factors must have been wanting in the two patients.

(VII) BLOOD AND DISEASE. Reference to the activities of leucocytes in the destruction of foreign bodies, including bacteria, in the blood-stream has already been made (page 328). In addition, the blood is able to produce substances which can protect the body against the possible ravages of invading germs. This is but one manifestation of a general property of the blood to react against large foreign carbohydrate or protein molecules and it will be convenient here to discuss the wider aspect of this behaviour.

Foreign substances in the blood, whether germs or other molecular aggregates, which induce such reactions by the blood are termed **antigens**, whilst the specific substances formed to combat them are called **antibodies**. When the offending particles are germs the antibodies may have recourse to one of three possible protective influences. They may (i) result in the neutralisation of the harmful substances, including the metabolic end-products (*toxins*) which may diffuse from the bodies of the germs into the bloodstream of the host, this being known as an *anti-toxic* effect; (ii) be responsible for rendering the invading germs more readily liable to destruction by phagocytes, by a sort of 'softening-up' process, this being *opsonification*; (iii) bring about the actual death of the germs, this process being termed *lysis*. In the case of anti-toxin production immunity may be acquired for some considerable time afterwards, due to the fact that the antibodies are formed in considerable excess over immediate requirements and are retained in the blood-stream subsequently.

Medical science has developed an elaborate technique of inducing artificial immunity against a number of the more serious diseases. Thus dead bodies of disease germs will act as antigens, stimulating the blood to the formation of the appropriate antibody. Immunisation against typhoid fever is achieved by the injection of typhoid germs killed by heat treatment. In other cases a 'weakened' form of the germ is used as the antigen. It is upon this principle that vaccination against smallpox depends. The vaccine employed is, in fact, the cowpox virus, obtained from inoculated calves, the effects of the virus in these animals being negligible. In man it induces the production of the smallpox antibody.

Passive immunisation is achieved by the injection of ready-made antibodies into the subject (in contrast with the example of *active* immunisation quoted above, where antigens induced the formation of antibodies by the subject's blood). It is normally of relatively short effectiveness and an example is provided by immunisation against diphtheria. Here the formation of the antibody is induced in the blood of the horse, this blood being subsequently drawn off and the antibody (antitoxin) removed, purified and standardised.

Indirectly concerned with health is the problem of **agglutination**, which frequently occurs when the blood of two persons is mixed. The investigation of this phenomenon was essential to the practice of blood transfusion. Agglutination manifests itself in the collection of erythrocytes in large masses, and on this basis there are four human blood groups. Four substances are involved, two agglutinable substances, or antigens, (*A* and *B*) in the erythrocytes and two agglutinators, or antibodies (α and β) in the plasma. The four blood groups are composed as follows, where + indicates the presence and − the absence of the various components of the system.

	A	*B*	α	β
Group *A*	+	−	−	+
Group *B*	−	+	+	−
Group *AB*	+	+	−	−
Group *O*	−	−	+	+

Agglutination results if either *A* and α or *B* and β are brought together, for in these conditions the antibodies adhere to the surface of the corpuscles, causing them to stick together in clumps. When a transfusion is undertaken it matters little if the donor's blood causes some agglutination of the recipient's erythrocytes, since the plasma of the donor's blood will become greatly diluted and agglutinate relatively few corpuscles. Thus, since the blood of members of group *O* contains no agglutinable substances, such persons are said to be *universal donors*, for their corpuscles cannot be made to agglutinate. In like manner, persons belonging to group *AB* are *universal recipients*, for their plasma contains no agglutinating agents. It is worthy of note that antigen *A* is now believed to exist in two forms, styled *A*1 and *A*2. It has been demonstrated that blood-groupings are inherited on a strictly Mendelian basis (see page 580).

(VIII) BLOOD AND BODY-TEMPERATURE. The blood is responsible for the distribution of heat evenly throughout the body. The maintenance of a constant body-temperature is a very important property of mammals and birds, and this is brought about by various means, dependent upon conditions.

Heat may be *lost* from the body of a mammal as a result of sweating.

Here water is withdrawn from the blood by the sweat glands and is passed up to the surface. The latent heat of evaporation is supplied by the body, which is thus cooled. The surface capillaries tend to dilate when the body is producing an excess of heat. This greater exposure of the blood results in the loss of heat. Heat is further lost in expiration, urination and defaecation.

Heat may be *conserved* within the body by the closure of the ducts of the sweat-glands and of the superficial blood-capillaries.

Finally, heat may be *gained* by means of physical exercise, an involuntary form of which is shivering. Man may further supplement this method by consuming more heat-producing foods, wearing suitable clothes and heating buildings. These methods must not be described as 'artificial'. They are merely the results of the great development of the cerebral cortex in Man, enabling him the more successfully to combat environmental conditions. They are, in fact, as 'natural' to a man as panting is, for example, to a dog.

(IX) ERECTION OF THE PENIS. This is brought about by the temporary collection of blood in blood-sinuses contained in special erectile tissue, composed largely of trabeculae of connective tissue.

Organs and Organ-systems

Differentiated cells come to take up a particular configuration within the animal or plant body, and a group of cells comprising a structure more or less clearly demarcated from other parts of the body and concerned with the performance of some specific function or functions constitutes an **organ**. Thus the heart, for example, is concerned with the pumping of blood. Its boundaries can be quite clearly defined, but it contains, as well as muscle-cells, a certain amount of connective tissue and epithelium. Similarly, a leaf, though consisting of several different types of cell, may be regarded as an organ of the body. The liver is an example of an organ associated with a number of diverse functions – e.g., the formation of urea, the secretion of bile and the storage of glycogen. But a complete function – e.g., digestion – may depend for its performance on a number of organs. Such a group of physiologically-related organs constitutes an **organ-system**. Thus the alimentary canal, together with the liver and pancreas, comprise the alimentary system, whilst the vascular system is composed of the heart, the arteries and the veins. This principle cannot be applied with much success to plants, even the higher ones, since individual functions are distributed more widely amongst the various parts of the body. Thus, for example, water and mineral salts are absorbed by the roots and conveyed by the xylem to the leaves. Here photosynthesis is effected, followed by distribution of carbohydrate material, principally in the phloem, where further chemical changes may occur. All these regions are concerned in the manipulation of food. No useful purpose is therefore served by any attempt to arrange organs,

themselves less clearly defined than in the animal, into functional systems.

Division of Labour in Animal Communities

So far the principle of division of labour has been considered only in so far as it applies to the organisation of an animal or plant body. Functions have become delegated, first to a few specialised cells, or parts of cells – e.g., the muscular portion of the musculo-epithelial cells, then to larger groups of cells, constituting an organ – e.g., the leaf of a plant – and finally to a composite organ-system. Some animals have, however, become associated in varying numbers to form communities, and the Honey Bee and White Ant will be considered as examples, indicating a new departure in the principle of division of labour.

(A) THE HONEY BEE. A typical hive contains but one queen, some six to eight hundred drones and fifteen to twenty thousand workers. In accordance with the social habits of this insect the three types of individual constituting the community have become functionally differentiated.

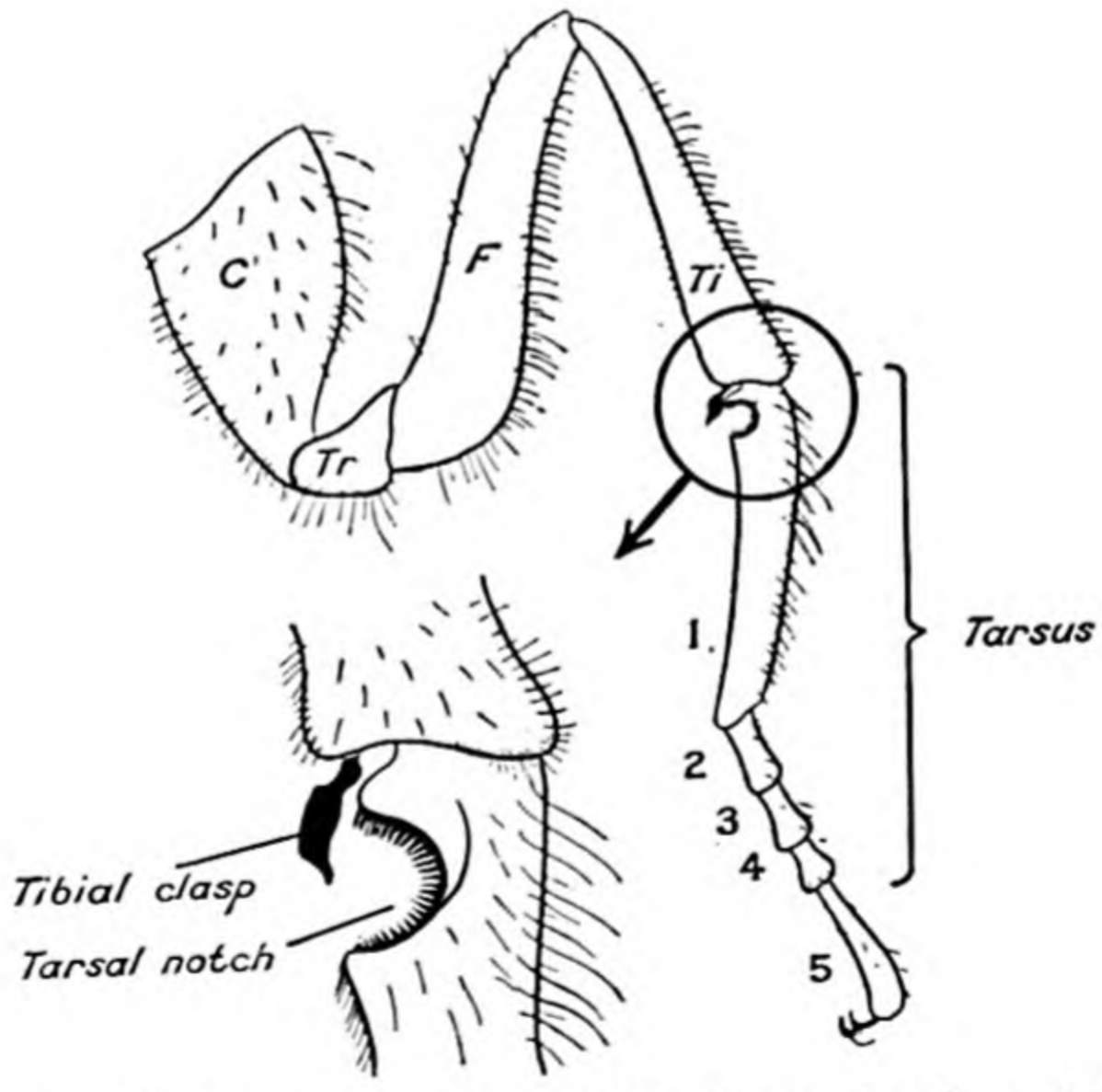


FIG. 236 – *Honey Bee*. The first leg. By drawing the antenna between the comb of the tarsal notch and the tibial clasp a cleaning action is effected. Key beneath Fig. 238.

The queen is the only functional female, being concerned solely with the deposition of eggs, which is effected by a secondary opening at the base of a long tube, the **ovipositor**, protruding from the tip of the abdomen.

The ovipositor is connected with a duct from a poison-gland, so that this organ functions as a sting. The workers, on the other hand, are sterile females, and the ovipositor of the queen here serves exclusively as a sting. Their bodies are modified for the collection of nectar and pollen, as well as for the construction of the combs. The legs exhibit various technical modifications. Those of the first and second legs are shown in Figs. 236 and 237. The third legs are especially well adapted to the temporary storage of pollen for transport, as indicated in Fig. 238. On the outer surface of each tibia is a deep concavity, termed a **corbiculum**, or **pollen basket**, fringed by a number of large, curved hairs. Ten rows of stiff

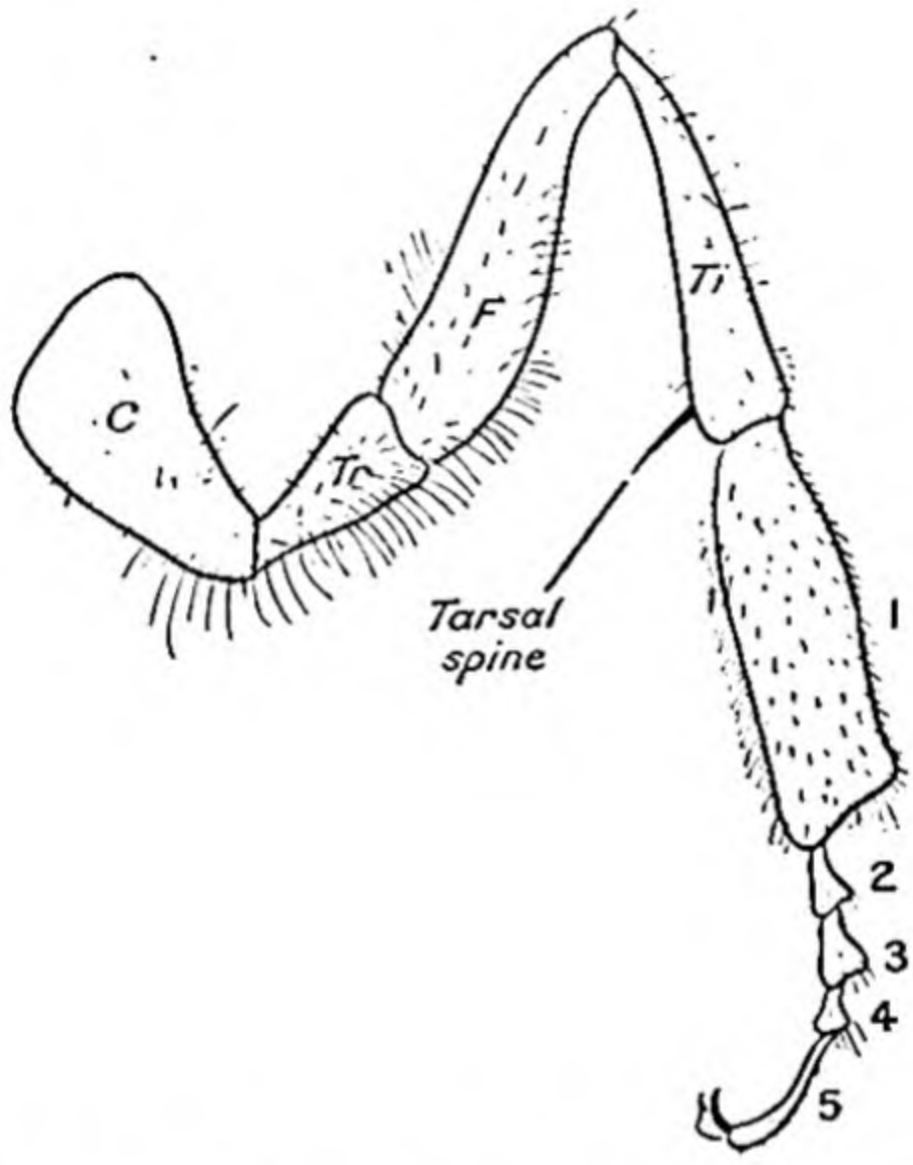


FIG. 237 – *Honey Bee.* The second leg. The tibial spine is used for loosening the pellets of pollen from the pollen baskets of the hind legs and also for cleaning the wings and spiracles. Key beneath Fig. 238.

spines on the basitarsus are used to collect pollen from the hairs of the body. When loaded, the leg of one side is rubbed against that of the other in such a manner that the tibial rake scrapes off the pollen. (These hairs are also used to remove wax scales from the abdomen and pass them to the mandibles.) The pollen so removed falls on to the auricle (Fig. 238, I). When the basitarsus is closed against the tibia the pollen is forced upwards and, being sticky, adheres to the limb. More pollen is successively packed into the lower end of the basket until it is full.

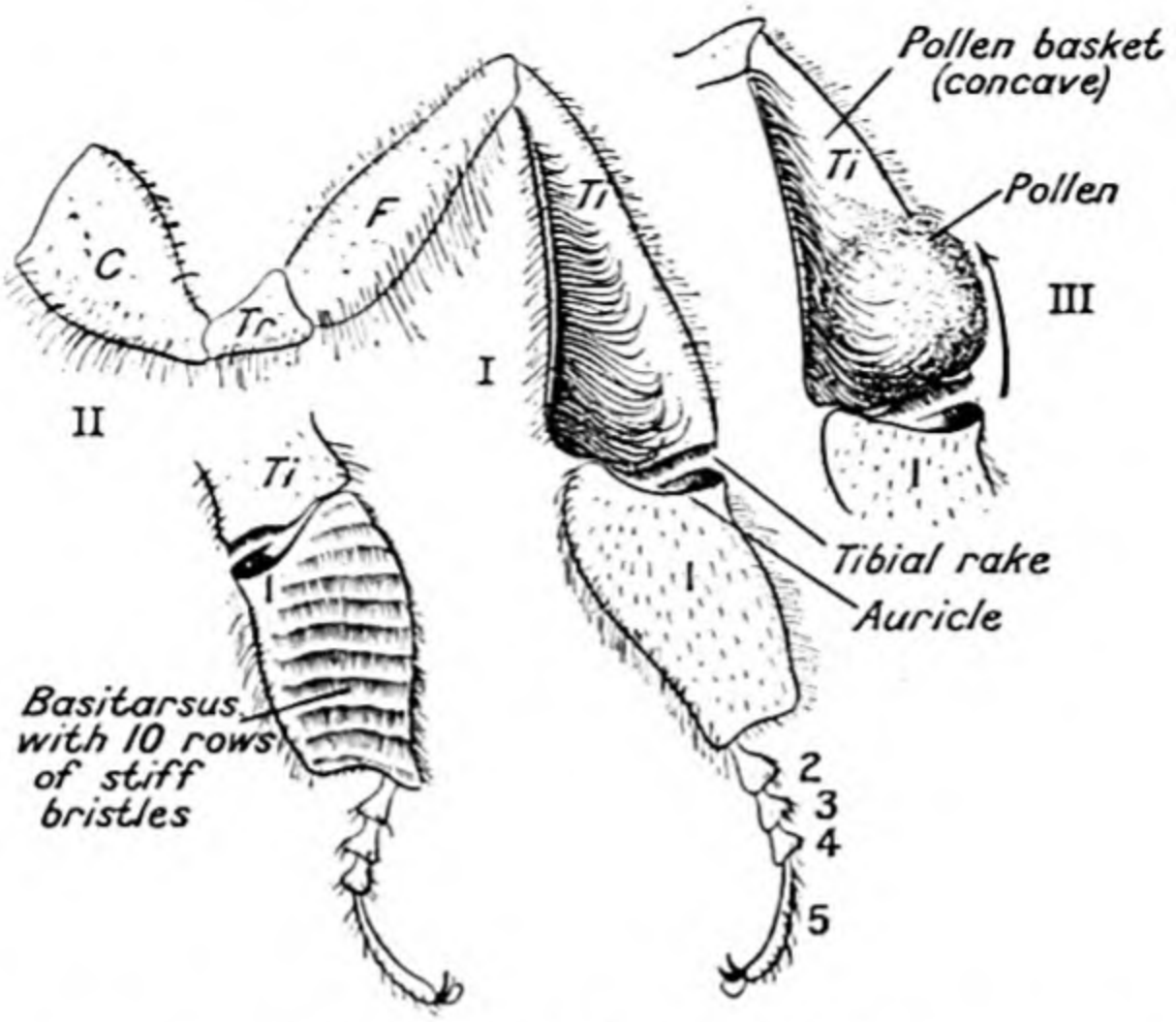


FIG. 238 – *Honey Bee.* The third leg
I., Entire; *II.*, Inner view of first tarsal joint (basitarsus); *III.*, Outer view of tibia, showing pollen basket. *C.*, Coxa; *F.*, Femur; *Ti.*, Tibia; *Tr.*, Trochanter; 1–5, Tarsals.

For the removal of nectar from the nectaries of flowers the mouth-parts have become modified to form a tubular structure, or **proboscis**. The sucking tube of this organ is formed by the elongation and fusion in the middle line of the laciniae of the labium (page 70), constituting the **ligula**. It is enclosed in a sheath, formed by the elongated maxillae.

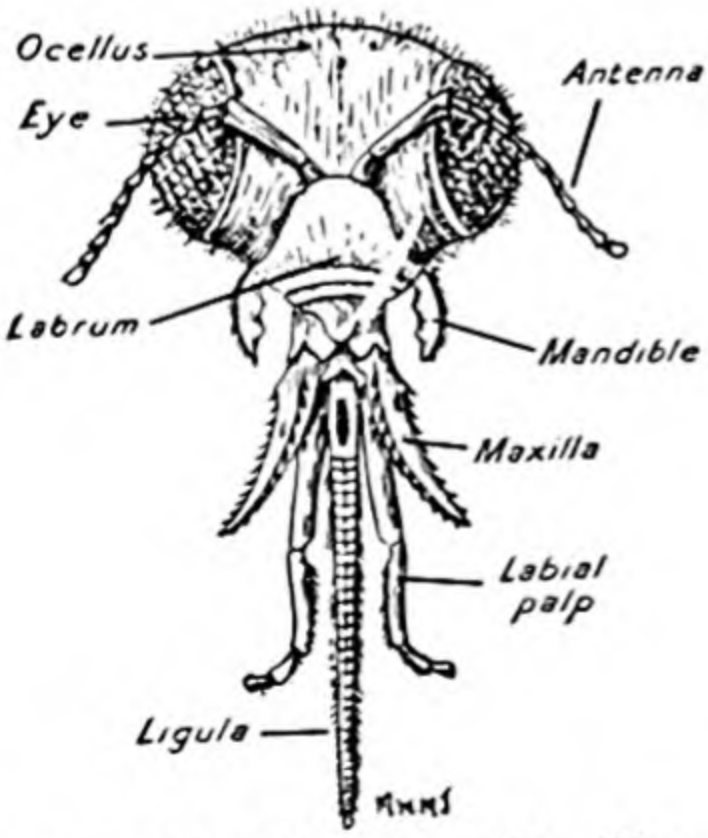


FIG. 239 – The Honey bee. The head.

The nectar obtained from flowers is converted into honey in the honey-stomach of the worker bee, corresponding to the crop of the cockroach. It is then regurgitated and deposited in the comb.

The construction of the comb by the workers is facilitated by further somatic modifications. On the ventral surface of the second to the fifth abdominal segments glands are found, concerned in the secretion of wax. This is produced in the form of plates, in which condition it is removed by spines on the first joint of the tarsus of each hind-leg to be conveyed to the mandibles, where it is moulded into

cells. The honeycomb so formed is remarkable in that its construction yields the maximum of space with the minimum expenditure of material. The cells are of hexagonal shape and are built in double series, placed back to back. The duties of the hive are shared by all the workers, the rearing of grubs being undertaken by the younger ones, which later in life become collectors.

Finally, the drones of a hive are the males. They contribute nothing to the maintenance of the community, and may properly be regarded as social parasites. They follow a young queen on her 'nuptial flight', and one of them eventually inseminates her. The supply of spermatozoa thus acquired is used for all subsequent fertilisation of eggs by the queen, which may live for as long as five years. At the advent of winter the drones are cast out of the hive, whilst the queen and workers survive on the store of honey.

Swarming

Only one queen at a time is tolerated in a hive. When, therefore, a young queen appears two alternatives are open. Either she and the old one fight to the death of one, or else the latter leaves the hive, followed by a large number of workers. This is the more usual procedure, and constitutes a swarm. It is either re-taken by man, or else a new nest is constructed by the workers in some suitable position, as, for example, in a hollow tree. It is important to notice that in this way the formation of new colonies is facilitated, and in this respect swarming may be compared with vegetative propagation in members of the plant kingdom. This is clearly seen, for example, in the reproduction of *Spirogyra* by fragmentation, for each portion can then give rise to a complete new filament. Similarly a potato plant may give rise to a number of tubers, each capable of growth into a new plant. By swarming, as by vegetative means, distribution is effected, thus facilitating reproduction.

(B) THE TERMITE. Termites, or White Ants, are social insects, chiefly confined to the tropics and found very commonly in West Africa. Their homes are constructed of hard material, sufficiently strong to withstand the combined weight of several men. They sometimes reach a height of twelve feet, and take the form of conical pyramids. Within, each is subdivided into a number of separate compartments, each associated with the performance of a particular service. Thus there may be identified the royal chamber, the workers' quarters, the nursery, food storehouses and ventilating chambers. In the royal chamber dwell the king and queen, the parents of the whole community. The queen deposits eggs, which are conveyed away by workers to the nursery, where development ensues. The workers tend the developing nymphs, wait on the king and queen, construct and repair the hive and secure the exit of certain mature, winged forms (see later) from the hive. As well as workers there are soldiers, whose function it is to defend the community, their mandibles

being modified to form large and powerful structures, whilst the skeletal armature of the head is especially well developed. Neither workers nor soldiers are fully developed sexually, whilst they are wingless. At the onset of the rainy season a number of winged forms are produced. These, when mature, leave their nest and eventually become parents of fresh communities. An important feature of the organisation of some nests is the production of a Fungus in the storehouses. The exact relationship between cultivator and crop is not fully known, and only recently has it been found possible to rear the Fungus in question outside the termitaria. It would appear that the insects provide it with the specific substances essential for life, whilst they themselves derive nutritive value from it. Thus there exists a reciprocity of benefit between Fungus and termite. The majority of termites are, however, wood-feeders, and in their gut dwell certain flagellate Protozoa (e.g. *Trichonympha*), largely responsible for the digestion of the cellulose.

In both instances outlined above, the division of labour characteristic of social life is accompanied by structural differentiations between various members of the community. In man this principle of division of labour is very highly organised, though not facilitated by anatomical adaptations. To a limited extent only the members of a human community may select tasks to which they are perhaps best fitted, though qualifications are often of a mental, rather than a purely physical, nature. By a materialistic interpretation even mental variations may be attributed to discrepancies in the physical structure of the cerebral cortex (page 472), though such modifications are not yet recognisable as such.

Individuality

This phenomenon of division of labour must necessarily influence the concept of individuality. In the Protozoa there is little difficulty in designating the term 'individual' to a whole organism. An amoeba, though non-cellular, is able to carry out all its life processes with the limited structure at its disposal. It is therefore an individual. At the other end of the scale the position is equally clear. Thus in an insect community or human society the attribution of individuality to separate organisms is not to be called in question, even though some members may be unable to perform certain essential functions. Thus drone bees, for example, play no part in the collection of food, and perish once they are ejected from the hive.

But between these two extremes lie various degrees of organisation such that individuality is not at first evident. Two examples will serve to illustrate the difficulty encountered. The first is the *Volvox* colony, and the other is drawn from *Obelia*. With the *Volvox* colony there are but two possibilities. Either the whole colony constitutes a single individual, or alternatively individuality must be assigned to each separate cell of the colony. In *Obelia* there are even more possibilities. The *Obelia* may be

considered as an individual, composed of its constituent hydranths and blastostyles. But if this be done, what of the medusa? In this connexion several suggestions may be made. (1) Since it carries out all processes essential to life it itself may be described as an individual. (2) Alternatively, it may be suggested that the whole and every part of the structure arising from the fertilised egg is an individual, in which case the medusa has no individuality apart from that of the polyp stock. (3) Finally it may be maintained that each polyp, including hydranths, blastostyles and medusea, is an individual. It is necessary now to discover which of the possibilities in the above examples it is most logical to adopt. For this a definition of an individual must be sought. There are three possible possibilities.

(*a*) An individual is the whole mass of protoplasm produced by division and development from a zygote. It requires very little consideration to demonstrate the untenability of this hypothesis. It would involve the deduction that all forms produced from a parent by asexual means comprise one aggregate individual. Asexual reproduction is common not only in the Protozoa, but in forms as high as insects eggs may develop without previous fertilisation. This is common in social forms – e.g. bees – and in aphides. Vegetative reproduction in plants renders this definition still further unacceptable. It would imply, for instance, that all the fruit trees of any one named variety were one composite individual.

(*b*) An individual is a structure capable of performing all the functions essential to life, except possibly that of reproduction. This view ignores the essential wholeness of, for example, an *Obelia* colony. By analogy with higher forms the blastostyles are morphologically organs, rather than distinct persons. They possess the power of budding off medusae, but depend for their supply of food on that transmitted to them from the hydranths via the hydrocaulus. Since the blastostyles cannot be regarded as individuals it is illogical to apply this term to the hydranths, which are obviously comparable structures.

(*c*) An individual is a continuous mass of living matter arising by fission. This is by far the most satisfactory definition. It involves the regarding of the entire *Obelia* as an individual, and likewise the *Volvox* colony. Each is produced by fission, and this concept of individuality is entirely in accordance with unpremeditated impressions, which frequently approximate very closely to the truth. On superficial examination an obelia or a volvox colony appears to be an individual. Each leads a separate existence, and is identifiable as a complete whole. The present definition of an individual obviously applies precisely to those particular features where preceding attempts have failed. That separate cells of a volvox colony could exist independently is a hypothesis: that they do not is a fact. Gametes (germ-cells) liberated from the body of the parent are to be regarded as individuals whose development is completed only after fusion of two of them.

PRACTICAL WORK

The majority of types mentioned in the foregoing chapter are described elsewhere, together with suggestions for practical work.

The detailed histology of *Hydra* and *Fucus* may well be revised here in connexion with the problem of cellular differentiation.

Examine specimens of worker, queen and drone bees. Sketch (in relative sizes). Examine and draw the modified legs of the workers. Examine a prepared slide of the mouth parts of the worker. Compare with those of the cockroach.

PART IV

Comparative Physiology

The material in Parts I, II and III is intended to provide the student with a means of acquiring a knowledge of the essentials of anatomy of animals and plants, treated individually. As a result some sort of generalised conception of animal and plant structure should be formulated. With this as a background it is now proposed to consider the performance of life-processes. This is known as **physiology**. As far as possible it will be dealt with comparatively in animals and plants, though fundamental discrepancies in structure often result in wide divergencies of function. Similar functions may be performed in essentially dissimilar manners – e.g. digestion and photosynthesis –, whilst some functions are the almost exclusive province of either animals or plants. Thus motility is a characteristic of animals, though represented in some of the simpler plants. Physiological processes, as well as being compared in animals and plants collectively, are also compared in the higher and lower forms of each group considered individually.

CHAPTER 22

Nutrition

It must be clearly understood at the outset that, so far as is known, the living organism obeys the laws of the remainder of the physical universe, and amongst them the Law of Conservation of Energy must be mentioned. The living organism is continuously undergoing chemical and physical changes, some of which absorb energy, whilst others radiate it. But the sum of these two groups of energy must always be zero. An organism builds up its food into compounds constituting its protoplasm, and this process absorbs energy. The energy thus acquired is locked up in the form of the potential energy of the complex molecules of chemical compounds. These subsequently undergo disruption, their stored energy being converted into kinetic form. The sum-total of these two processes of synthesis and decomposition constitutes **metabolism**, sharply divisible into two phases. Thus processes involving the building up of the body and the assimilation of energy are grouped as **anabolism**, whilst **katabolism** is characterised by a breaking down of body-substance, accompanied by the liberation of energy. Nutrition, therefore, is concerned with the anabolic phase of metabolism.

Food of Animals and Plants

In respect of food animals and plants may be sharply contrasted. Thus the food of animals is essentially organic and is taken mostly in solid form, whilst that of plants consists of simple materials absorbed in the liquid and gaseous states.

Food of Animals

There are six groups of animal food, classified according to their chemical constitution. They are

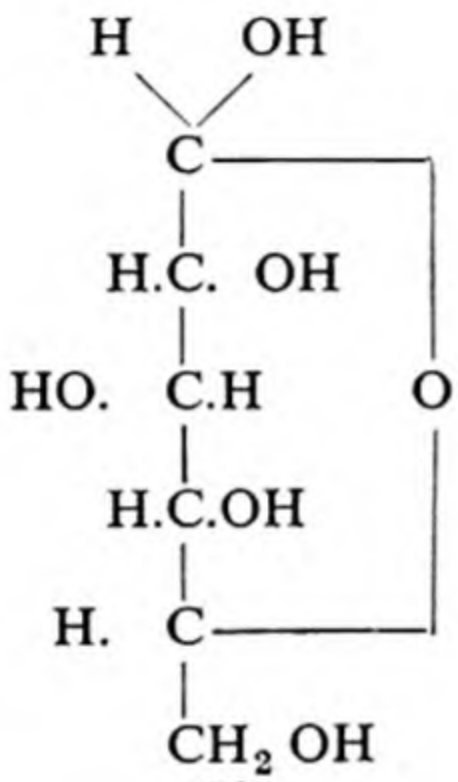
(*a*) Carbohydrates.
(*b*) Proteins.
(*c*) Fats.
(*d*) Vitamins.
(*e*) Mineral salts.
(*f*) Water.

They will be considered individually.

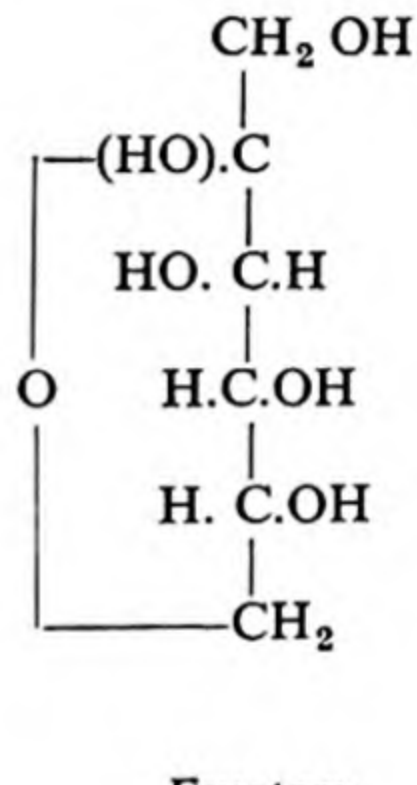
(A) CARBOHYDRATES. Carbohydrates are compounds containing only carbon, hydrogen and oxygen, the numbers of hydrogen and oxygen atoms in the molecule being in the ratio of two to one. They

are further subdivided into monosaccharides, disaccharides and polysaccharides.

(i) *Monosaccharides* have the general formula $C_nH_{2n}O_n$, where n ranges from 2 to 10. By far the most important are the hexose sugars, of formula $C_6H_{12}O_6$. The two best-known of these are glucose and fructose. Glucose occurs in fruit, in blood and other tissue-fluids of animals and is an end-product of carboyhdrate digestion. Fructose also occurs in fruits, and is an important constituent of honey. The formulae of these sugars are as follows:



Glucose



Fructose

Thus, with reagents strong enough to break the ring, glucose will act as an aldehyde and fructose as a ketone, and they differ from each other as an aldehyde differs from a ketone. Since they both contain a $-CH_2OH$ group they are capable of acting as primary alcohols as well as secondary, the $>$ CH.OH group also being present.

(ii) *Disaccharides* are most commonly formed as a result of condensation of two molecules of a hexose – i.e. they combine with the elimination of water. Thus:

$$2C_6H_{12}O_6 = C_{12}H_{22}O_{11} + H_2O.$$

If they retain the aldehydic or ketonic groups they behave somewhat similarly to the monosaccharides. The two most important having these properties are maltose and lactose. Maltose occurs in malt and is formed by the hydrolysis of starch and glycogen, whereas lactose is the sugar of milk and is readily converted by bacterial action to lactic acid, as when milk goes sour. On hydrolysis lactose yields glucose and galactose, whilst maltose produces only glucose. Sucrose, or cane-sugar, is perhaps the commonest disaccharide.

(iii) *Polysaccharides* have the general formula $(C_6H_{10}O_5)_n$, where n

is of such value that the molecular weights range from 1,600 to 30,000. They occur commonly in plants, the best-known forms being starch, cellulose and inulin, whilst the glycogen of animals belongs to the same class. On hydrolysis they eventually produce monosaccharides.

(B) PROTEINS. Proteins are complex chemical substances occurring naturally and formed by the condensation of amino-acids. They all contain carbon, hydrogen, oxygen and nitrogen, and possibly, in addition, sulphur and phosphorus. The chemical structure of proteins may best be appreciated by a consideration of their formation from the simplest of their derivatives – an amino-acid. This is an amino-derivative of a fatty acid, and may be given the general formula $R.CH.NH_2.COOH$. Two of these may condense together with the formation of a peptide, as shown.

$$\begin{array}{l} R.CH.NH_2.CO.OH + H.NH \\ \qquad\qquad\qquad\quad | \\ \qquad\qquad\qquad R.CH.COOH \end{array} = \begin{array}{l} R.CH—CO—NH \\ \qquad\quad | \\ \qquad NH_2 \end{array} \quad \begin{array}{l} \\ | \\ R.CH.COOH \end{array} + H_2O$$

Peptide

Further condensation between two or more peptide molecules will result in the formation of a protein.

$$\begin{array}{l} R.CH.CO.NH \\ \quad | \\ NH_2 \end{array} \quad \begin{array}{l} \\ | \\ R.CH.CO.OH \end{array} + \begin{array}{l} R.CH.CO.NH \\ \quad | \\ H.NH \end{array} \quad \begin{array}{l} \\ | \\ R.CH.COOH \end{array} =$$

$$\begin{array}{l} R.CH.CO.NH \quad R.CH.CO.NH \\ \quad | \qquad\quad | \\ NH_2 \quad R.CH.CO. \end{array} \quad \begin{array}{l} \\ | \\ NH.R. \end{array} \quad \begin{array}{l} \\ | \\ CH.COOH \end{array} + H_2O$$

A simple protein molecule.

There are, in all, some twenty amino-acids, with molecular weights ranging for 75 to 204. Proteins themselves are formed by linkage of from fifty to five thousand amino-acids. Thus for a protein composed of fifty amino-acids of all twenty different kinds there are 20^{50} possibilities for its structure. The specificity of proteins is referred to again on page 515. ^{14}C has been intensively employed in protein investigation. On hydrolysis a protein is converted first to a peptide and then to an amino-acid.

Proteins are essential constituents of protoplasm, and tests for their identification will be found at the end of the present chapter.

(C) FATS. Fats are esters formed between the higher fatty acids and aliphatic alcohols. The commonest are those formed between glycerol and the higher fatty acids, of general formula $C_nH_{2n+1}COOH$. Thus the general formula for a fat may be represented as below, the equation showing the result of hydrolysis of such a fat.

$$\begin{array}{l} CH_2.O.OC.C_nH_{2n+1} \\ | \\ CH.O.OC.C_nH_{2n+1} \\ | \\ CH_2.O.OC.C_nH_{2n+1} \end{array} + 3H_2O = \begin{array}{l} CH_2OH \\ | \\ CH.OH \\ | \\ CH_2OH \end{array} + 3C_nH_{2n1}COOH$$

Fat *Glycerol* *Fatty acid*

The most commonly occurring fats are palmitin and stearin, found in animal and vegetable tissues. Their formulae may be derived from the above general formula by assigning to *n* the values 15 and 17 respectively. Certain unsaturated acids, of general formula $C_nH_{2n-1}COOH$, form oils with glycerol, and these fats are also widely distributed in animal and plant bodies. The commonest is olein, oleic acid having the formula $C_{17}H_{33}COOH$. Structurally it may be represented as

$$CH_3.(CH_2)_7.CH{=}CH.(CH_2)_7COOH$$

Oleic acid

Since it is a monobasic acid three molecules of it will condense with one molecule of glycerol, forming one molecule of olein.

(D) VITAMINS. Vitamins are essential in minute quantities to at any rate the higher animals, possibly for life and certainly for the maintenance of a healthy condition. They occur in the living tissues of animals and plants, and have been isolated, and in some cases synthesised. They are divisible into two classes, namely fat-soluble and water-soluble, according to the medium which serves as a solvent for them.

In the table (page 373) in which the chief physiological properties of the principal vitamins are summarised, vitamins *A* to *K* (inclusive) are fat-soluble and the remainder water-soluble.

In conclusion, interesting facts about two of the vitamins should be noted.

Vitamin *D* is produced as a result of the effects of solar or ultra-violet irradiation of a precursor, known as *ergosterol*. This is found commonly in Fungi, higher plants and the liver-oils and nervous tissue of animals.

Vitamin *C* is unstable in alkaline solution, particularly in the presence of oxygen. The practice of adding soda to the water in which green vegetables are cooked, for the purpose of 'improving the colour', is greatly to be deprecated.

(E) MINERAL SALTS. Mineral salts are an essential constituent of the animal body. A remarkable fact was elucidated in the early part of the present century, namely that the concentration of salts in the plasma in the blood of vertebrates, and of invertebrates with a closed vascular system, closely resembles that of sea-water diluted to one-third of its usual concentration. It is presumed that this is on account of their evolution from forms whose body-fluids were practically in open contact

with the sea, and that when these ancestors lived the concentration of salts in the sea was only one-third of its present value. There is no doubt that certain ions play an important role in the regulation of the animal organism, the chief ones being hydrogen, bicarbonate, phosphate, calcium, magnesium, sodium, potassium, iron, sulphate, chloride and iodide. Their significance and form of occurrence may best be summarised in the form of a table (page 374).

Vitamin	Common Name	Function	Deficiency Effects	Natural Sources
A	Axerophthol	Epithelial development	Epithelia become hardened: malformation of bones	Liver-oils, butter, eggs, cream, green vegetables
D2 D3	Calciferol (from erogsterol by irradiation)	Calcium and phosphorus metabolism	Rickets: poor teeth	As *A*, plus ergosterol
E	α-tocopherol	Fertility	Abortion in female: loss of fertility in male	Meats, eggs, green vegetables
K	Phylloquinone	Clotting of blood	Haemophilia	Lettuce, kale, spinach, pig-liver, tomatoes
B1	Aneurin	Carbohydrate metabolism	Neuritis: beri-beri	Yeast, whole cereals, pig-liver, nuts, eggs, legumes
B2	Riboflavin	Carbohydrate absorption	Poor retinal pigments – impaired vision	Milk, yeast, liver, meat, eggs, cheese
B3 B5	Pantothenic acid Nicotinic acid	Carbohydrate and protein metabolism	Dermatitis: digestive and nervous disorders	Yeast, liver, eggs, kidney, meat, green vegetables
B6	Pyridoxin	Fat and protein metabolism	Dermatitis: anaemia	Yeast, liver
H	Biotin		Dermatitis: lassitude	Liver, kidney, eggs, milk, green vegetables
C	Ascorbic acid	Healing of wounds and fractures	Capillary-resistance: scurvy; haemorrhage	Oranges, lemons, raw vegetables
P	Citrin	As *C*	As *C*	As *C*, grapes
M?	Folic acid	Erythrocyte-formation	Anaemia	Liver, yeast, green leaves, spinach
	Inositol	Fat metabolism	Loss of hair	Cereal grains, liver

(F) WATER. Water is the chief quantitative constituent of living matter. The weight of water in a living organism varies from 60% to 95% of the total. It may be either free, acting merely as a solvent or bound, in which case it is combined with tissue colloids. Water serves a number of purposes in the animal body. It forms the bulk of the structure, rendering the organism plastic but incompressible. It serves as a solvent, as well as accommodating the assimilation of foods, for all reactions

Ion	Form in which present in food	Function
Hydrogen	Water and acid salts	Essential constituent of water and organic foods. H ion concentration regulates heart-beat, respiration and enzymes
Bicarbonate	Acid Na and Ca carbonates	Regulation of H ion concentration
Phosphate	Acid Ca and Mg phosphates	Regulation of H ion concentration. Hardening of bones
Calcium	Acid phosphate and carbonate	Coagulation of blood. Hardening of bones
Magnesium	Acid phosphate	Hardening of bones
Sodium	Chloride and acid phosphate	Muscular contraction
Iron	Organic compounds and inorganic salts	Constituent of haemoglobin
Sulphate	Sulphates and sulphoproteins	Frequent constituent of proteins
Chloride	Sodium chloride	Controls osmosis. Constituent of hydrochloric acid of stomach
Iodide	Iodides	Constituent of thyroxin (page 479)

involved in this process take place in aqueous solution. Many waste products are conveyed to the exterior in aqueous solution. Water also plays an important part in the regulation of body-temperature in mammals. Since it has so high a specific heat a great deal of heat must be lost before the temperature of the body falls appreciably, whilst when water is evaporated at the surface very efficient cooling occurs, since the latent heat of vaporisation is so high. Water is also of significance on account of the fact that waste carbon dioxide dissolves in it to form carbonic acid. From this hydrogen ions are set free. Thus when muscular activity is increased there is a corresponding rise in the output of carbon dioxide, and hence in the concentration of hydrogen ions. Accordingly both respiration and heart-beat are increased in rate.

In conclusion it will be appropriate to consider briefly the contents of one of the most natural of 'natural' foods, namely milk, with special reference to that of cows. All classes of food substance are represented. A rough analysis by weight shows 87.5% water, protein 3.3%, fat 3.7%, carbohydrate 4.7% and mineral salts 0.8%, with traces of vitamins. The carbohydrate is the disaccharide *lactose*, possessed of very limited

sweetening properties. Upon hydrolysis (page 389) it yields glucose and galactose in equimolecular proportions. The souring of milk is caused by the conversion of lactose to lactic acid, which then brings about the coagulation of the milk protein, *caseinogen*. This protein is itself rich in phosphorus. The rennin of the gastric juice (page 390) causes the conversion of soluble caseinogen into insoluble *casein*, which combines with calcium salts to form a clot. In addition to caseinogen, though in smaller quantities, milk contains *lactalbumen* and *lactoglobulin*, both similar in composition to egg albumen. It is these proteins which, when milk is heated, coagulate to form the characteristic 'skin'. The fat is present in the form of an emulsion, most of the globules of which rise to the surface when milk is allowed to stand, forming the cream. Chemically the fats are esters of glycerol, mainly with oleic and butyric acid. The principal mineral elements represented in milk are phosphorus and calcium; the iron content is surprisingly low. Finally, vitamins are widely present in milk, although the amounts eventually available to human beings largely depend upon the treatment which the milk has received between cow and consumer. In general, heat treatment and exposure to sunlight cause destruction of vitamins. Vitamins *A*, *B2*, *B5*, *C*, *D* and *H* (page 373) are present in varying amounts.

The biological significance of milk as a natural food is at once apparent. It contains virtually all essential ingredients of a balanced diet in easily digestible form and its supply to young mammals from their mother is practically ensured. Man has adapted this natural function in the case of the cow to meet some of his own nutritional needs.

Food of Plants

Green plants require as food the water and mineral salts absorbed by the roots from the soil, and the carbon dioxide entering the leaves from the air. Of water and carbon dioxide more will be said later. It is necessary here to notice what mineral elements are essential to healthy growth, and the forms in which they are usually absorbed. Of the mineral elements essential to plant growth, some are required in relatively large quantities. These major elements (macro-elements, or macro-nutrients) are nitrogen, phosphorus, potassium, calcium, magnesium, sulphur and iron. The ions most commonly occuring in the soil and supplying these elements are potassium, magnesium, sulphur and iron, phosphate, nitrate, and sulphate. Nitrogen is an invariable, and sulphur and phosphorus each a very frequent, constituent of proteins, and therefore in their absence growth soon ceases. Phosphorus is also required for the formation of nucleic acids, *A.T.P.* and *A.D.P.* (page 436). Magnesium is a constituent of chlorophyll (page 395), whilst iron, though not entering into the final composition of this pigment, is essential to the formation of a precursor, in which capacity it is dependent upon the presence of phosphate ions. Iron is also a constituent of cytochrome

(page 433). The successful formation of chlorophyll also requires the presence of calcium and potassium ions in balanced concentrations. The potassium ion also has a catalytic effect on some aspects of plant metabolism, for, in its deficiency, photosynthesis and protein synthesis are inhibited, whilst tissue respiration is accelerated. The significance of calcium in the formation of calcium pectate is now partly discredited, since this substance is not so universally distributed in cell-walls as was previously believed. It is more likely that the balance between bivalent calcium ions and monovalent potassium ions is required to maintain the differential permeability of cell-membranes, and hence to regulate turgor.

In addition to the elements named above, certain others, known as *trace elements*, are required in minute quantities for successful growth. So delicate have become the methods of detection and estimation of the importance of individual elements that experimenters can state that no element can be dismissed as inessential if it is present in a concentration greater than one part in a billion. Those elements upon which most work has been done are boron, zinc, manganese and copper. Broad beans grown in solutions spectroscopically free from boron fail to complete development, but if present in concentrations greater than 200 parts per million damage is caused. Boron has also been shown essential for the successful growth of tomatoes and sugar-beet. Algerian oats have been shown to suffer from a disease known as 'grey-speck' if deprived of manganese, whilst apple trees appear to require traces of zinc. Startling results have been obtained in work on lettuce by the inclusion of other elements in the nutrient fluid – e.g., nickel, cobalt, molybdenum, vanadium, chromium, tungsten and titanium. In general, it is believed that micronutrients (trace elements) participate in enzyme reactions in one of two ways:

(1) To act as electron carriers by virtue of valency changes. (This applies to iron also.)

(2) For the formation of intermediate compounds with substrate-enzyme complexes.

Bios

The nearest approach in plants to the vitamins of animals is a complex of substances believed to be necessary for the successful growth of yeast. Vitamins are, like hormones, trace substances, but they differ in that they must be provided by the environment, whereas hormones are elaborated internally. Some wild yeasts appear to be able to live on a diet composed exclusively of sugars and inorganic salts (notably ammonium phosphate): from these they may be able to manufacture their own bios. But many cultivated forms exhibit synthetic disabilities, and traces of organic substances have to be supplied. Among these are *inositol*, *biotin* $C_{10}H_{16}O_3N_2S$ – the vitamin *H* of animals), *nicotinic acid*, *riboflavin* (vitamin B_2), *pantothenic acid* and *pyridoxin* (vitamin B_6).

Absorption by Plants

It has been discovered that when a solution of certain substances is separated from the pure solvent by special membranes the membrane will permit the passage through it of the solvent molecules, but not of those of the solute. As a result water diffuses into the solution, say of sugar, tending to dilute it. This phenomenon is known as **osmosis**, and may be demonstrated by means of the apparatus shown in the accompanying figure. If a 1 % solution of cane-sugar be employed water would theoretically continue to enter until a column nearly seven hundred centimetres high were supported. In practice no membrane is sufficiently perfect to give the ideal result nor, if it were, could it be sufficiently securely affixed in the apparatus shown, where a pig bladder membrane is normally employed, to withstand the pressure set up. Precipitation membranes in the walls of porous pots are more stable and efficient. Such are exemplified by cupric ferrocyanide, obtained by filling a porous pot with copper sulphate solution and standing it in a vessel containing potassium ferrocyanide solution, both solutions being rather stronger than decinormal. The two solutions diffuse into the pores of the pot and form a precipitate of cupric ferrocyanide on contact. Best results are obtained if the diffusion is assisted by electrolysis, using a platinum electrode in the copper sulphate solution and a copper electrode in the potassium ferrocyanide solution.

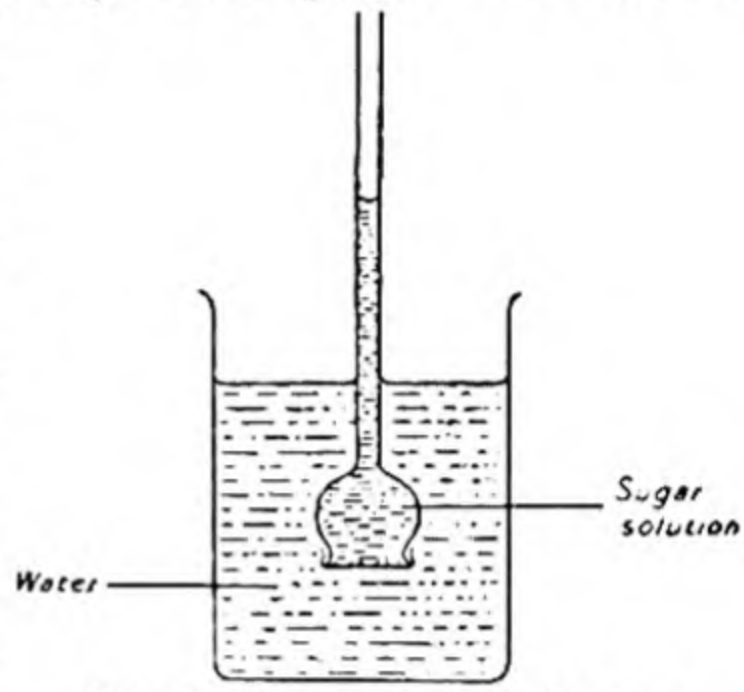


FIG. 240 – Apparatus for the demonstration of osmosis.

Alternatively, eggs may be employed for the demonstration of osmosis.

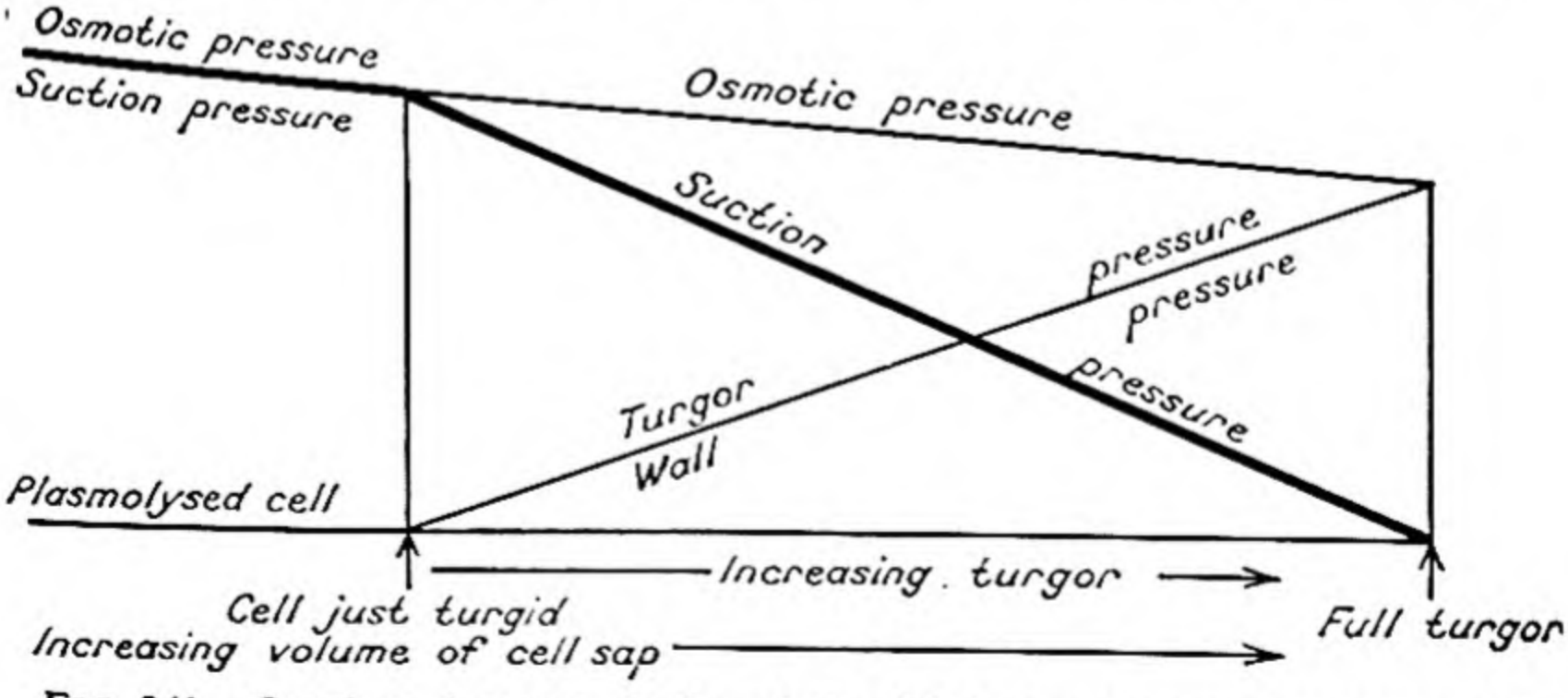


FIG. 241 – Graph to demonstrate the relationship between osmotic, turgor, wall and suction pressures.

The shells of two eggs are removed by immersion in hydrochloric acid, after which the eggs are thoroughly washed. One is then placed in water and the other in strong salt solution. The former expands considerably, whilst the contents of the latter shrivel away from the shell membranes, which are themselves responsible for the occurrence of osmosis. The pressure generated by the pure solvent in attempting to enter the solution is known as **osmotic pressure**, whilst the membrane allowing of the passage of solvent molecules only is said to be **semi-permeable**.

It will at once be apparent that this phenomenon of osmosis is applicable to the problem of the entry of water, adhering to the soil particles, into the cell-sap of the root-hairs. Soil-water is a dilute solution of mineral salts, whilst cell-sap is a comparatively concentrated solution of various solutes, predominant amongst which are sugars. The semi-permeable membrane is provided, not by the cellulose cell-wall, but by its protoplasmic lining. Nor is it completely semi-permeable, for it will permit the diffusion of dissolved mineral salts as well as that of the pure solvent: it may be described as selectively permeable. Thus water and dissolved salts will tend to move from the soil into the cell-sap of the root-hair. It should, however, be noted that there is considerable evidence that an active process is involved in the entry of water, with passive osmosis not solely responsible.

But another factor must be taken into consideration, and that is the pressure exerted by the elastic cell-wall as a result of the increasing sap-content of the cell. This is known as **turgor (= wall) pressure**, and will obviously tend to prevent the entry of water. An analogy may be drawn with a bicycle tyre and inner tube. The point of complete deflation represents a plasmolysed cell, where the vacuole is empty. As the inner tube is inflated, a point is reached where the inner tube just begins to bear upon the inside of the cover. This is equivalent to the beginning of turgor, and the pressure exerted by the tube on the cover is equivalent to turgor pressure. The cover resists the expansion of the tube by an equal and opposite force, which is equivalent to wall pressure. Resistance to inflation steadily increases, which is comparable with the fall in suction pressure of the cell upon the entry of more water. The resultant pressure available for the drawing in of water is known as **suction pressure** and represents the osmotic pressure of the cell-sap *minus* the turgor pressure. The relation between these three pressures is clearly indicated in the accompanying figure (page 377). Thus, if *S.P.* = Suction pressure, $O.P._{(Int)}$ = Osmotic pressure of sap, $O.P._{(Ext)}$ = Osmotic pressure of external medium, *T.P.* = Turgor pressure, *W.P.* = Wall pressure, then –

(1) For a cell in pure water –

$$S.P. = O.P._{(Int)} - W.P.$$

(2) For a cell in a hypotonic solution –

$$S.P. = (O.P._{[Int]} - O.P._{[Ext]}) - W.P.$$

At all times, *W.P.* is equal in magnitude to *T.P.* but opposite in direction of operation.

Once thus within the root-hair it is possible that the suction (not merely the osmotic) pressure there may be less than it is in the neighbouring cells of the cortex. Accordingly water will pass into the latter, and by a similar explanation its passage across the root to the outer surface of the xylem vessels may be accounted for. In other words, there exists a rising suction pressure gradient from the root-hair to the xylem.

The passage of water and its dissolved salts into the xylem has not been altogether satisfactorily explained. There can be no turgor in the vessels,

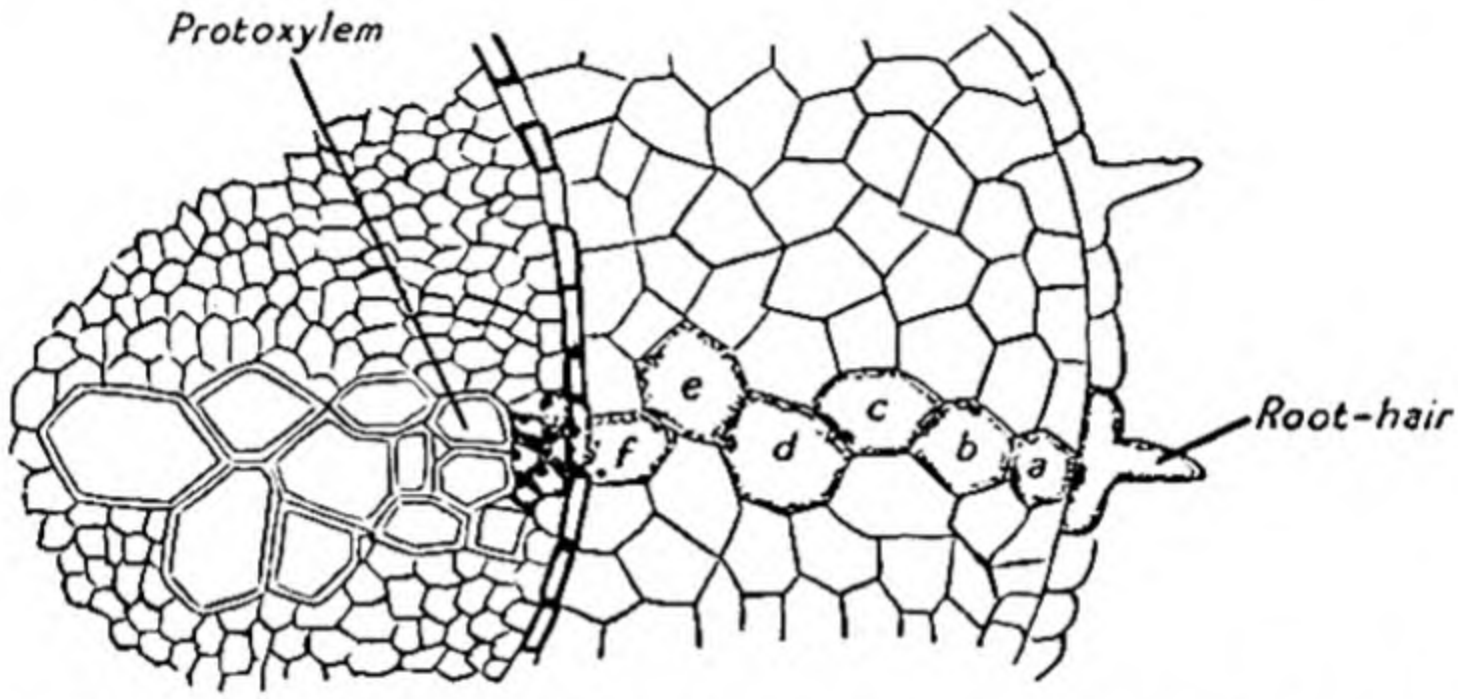


FIG. 242 – Transverse section of a portion of a root to show the direction of entry of water.

but their osmotic pressure is almost certainly lower than the suction pressure in neighbouring cells. It has been suggested that in the case of the cells abutting on to the xylem vessels there is a differential suction pressure, high towards the outside and low towards the vessel-surface, thus forcing water into the xylem. Alternatively, it may be that the explanation is the obvious and simple one, as suggested by the late Professor Maskell, who took the view that no difficulty existed here and that water entered the xylem as a result of the upward suction exerted by transpiration (page 380).

Once within the xylem vessels the water has to be raised to the leaves before it is utilised by the plant. This obviously presents some difficulty, especially to a plant of considerable height. One of the forces responsible for its accomplishment is the pressure exerted as a result of transpiration from the leaves. Such evaporation raises the suction pressure in the mesophyll cells, which consequently absorb water from surrounding cells. This results eventually in the withdrawal of water from the xylem of the veins, so that water from the stem is drawn up to replace it. This is partly facilitated by the so-called tensile strength of water, whereby it has been found possible for columns of water to depend in tubes of

considerable length without fracture. The passage of water up the stem of the plant is further assisted by the natural capillarity due to the narrow bore of the xylem vessels. This may be observed by placing the end of a capillary tube into a vessel containing a coloured liquid, when it will be seen that the level of the liquid in the tube rapidly becomes higher than that in the vessel. Finally there is a phenomenon to which the term **root pressure** is applied. Water is forced from the parenchymatous cells into the xylem vessels under considerable pressure, and as more passes in that previously there is forced further up the stem. It should, however, be noted that not all plants exhibit root pressure. Furthermore, where it does exist there is no variation in its magnitude with seasonal changes in the rate of ascent of sap.

To sum up, water is passed from the soil into the root-hairs as a result of the suction pressure exerted by the latter, and by a similar mechanism it makes its way across the tissues of the root. It may be mentioned here that the majority of the cells of the endodermis are impermeable to water, so that the passage of water through this layer is confined to a few cells which retain their thin, permeable walls: they are consequently known as **passage-cells**. Once the water reaches the outer surface of the xylem it is transferred to the tracheids and vessels by a mechanism not properly understood, whilst it finally makes its way up the plant in the xylem as a result of root pressure, capillarity and the transpiration current.

Transpiration

Mention has been made above of the importance of the transpiration current in the drawing of water up the plant, and it will be well therefore to consider this phenomenon in a little more detail here. The overall process of transpiration is divisible into a number of clearly defined stages. It consists first of the evaporation of water from the moist walls of the mesophyll cells. This results in the saturation of the air in the intercellular space system. In consequence there is diffusion of water vapour through the stomata when the external atmosphere has a saturation deficit – in other words, when a concentration gradient exists favouring outward diffusion. The rate at which this occurs is regulated by a number of factors. The humidity of the atmosphere will obviously exert an appreciable effect, for the higher its water-vapour content the less will be the rate of diffusion from the leaves. But even in a saturated atmosphere there will be some transpiration, since the temperature of the mesophyll cells will always be a little higher than that of the surrounding air, owing to their respiratory process. Wind, on the other hand, will tend to prevent an accumulation of water-vapour round the plant, so that transpiration will be encouraged. Temperature is effective in so far as it affects the saturation pressure of the atmosphere. The higher the temperature the greater will be the water-loss owing to transpiration. Light controls transpiration indirectly, for it has a direct effect on the condition of the

stomata, a phenomenon which will be considered in Chapter 23. In general the stomata remain open in light and close in darkness, so that transpiration must be slower at night. As well as acting in this way, it has been estimated that as much as 70% of the light-energy absorbed by the insolated leaves of a plant may be converted into the latent heat of evaporation of water, thus greatly accelerating transpiration.

There are conflicting views as to the value of transpiration to the plant. It is admitted (page 382) that the artificial reduction of its rate does not adversely affect the uptake of mineral salts. Indeed, some authorities claim that there is no evidence that it serves any useful function whatever, regarding it merely as the inevitable outcome of the construction and metabolic requirements of the plant. These same authorities believe that any lowering of leaf temperature is insignificant. In other words, flowering plants survive in spite of transpiration, rather than because of it.

Hydathodes

Sometimes it is necessary for the loss of water to continue even when the stomata are closed, for, owing to root pressure, water may still be passing up the xylem vessels. The excess moisture is eliminated through special organs, known as **hydathodes**. They are normally situated at the margins of the leaves, usually near the edges of the main veins. They may be discovered by placing a plant – e.g. a nasturtium – which has been well watered, beneath a bell-jar in a warm, moist atmosphere. Droplets of water appear on the leaves, indicating the position of the hydathodes. The commonest form of hydathode communicates with the exterior by a **water pore**. This lies in the epidermis, and to some extent resembles a permanently-opened stoma. Between the water pore and the end of the nearest vascular bundle is a mass of small-celled tissue, known as the **epithem**. The hydathode of the lesser celandine is of this type, and is shown in longitudinal section in Fig. 243.

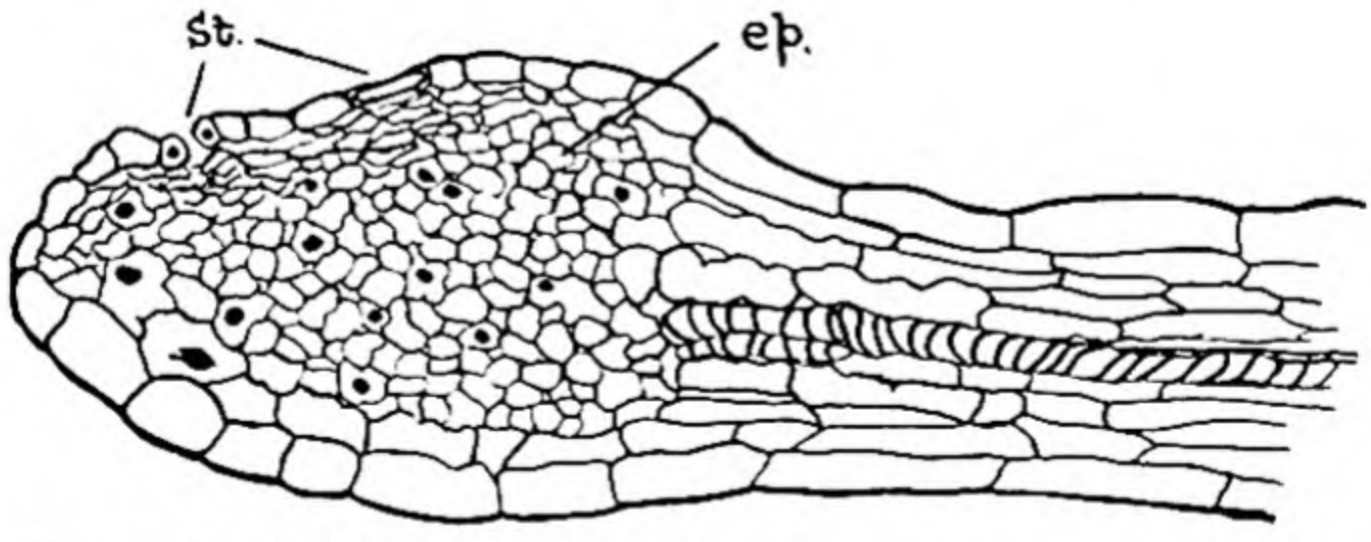


FIG. 243 – Hydathode of Lesser Celandine (*Ficaria verna*) in vertical section. (After Salisbury.)
ep., epithem tissue; *St.*, water-pores.

Alternatively the hydathode may take the form of a glandular hair, as shown in Fig. 244. This type occurs, for example, in the runner bean.

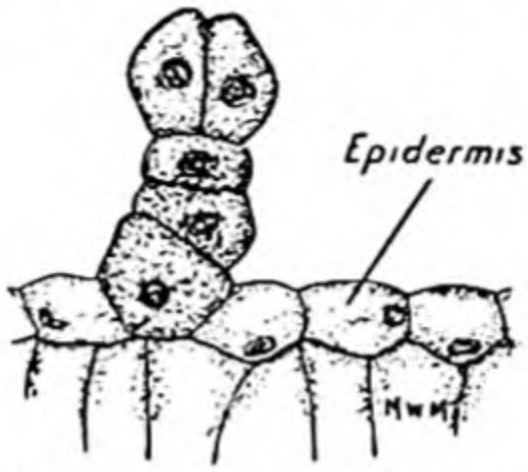


FIG. 244 – Hydathode of the glandular hair type.

Absorption of Mineral Salts

To account for the absorption of mineral salts some mechanism other than passive entry with water must be invoked, since artificial reduction of the rate of transpiration does not appear to reduce the rate of uptake of mineral salts. Furthermore, absorption may continue even though the concentration of ions in cell-vacuoles be higher than in the external medium. Energy is obviously required for the process, since in roots inadequately aerated – e.g., in artificial cultures unless special precautions are taken – the rate of entry of ions is greatly depressed. To some extent the rate of intake of salts into a tissue does depend upon the internal concentration of those salts. In many cases this factor is very specific – e.g., the rate of entry of nitrate and phosphate ions depends upon the internal concentration of *those ions*, and not upon that of ions generally. Since ions are conducted fairly rapidly away from roots to other parts of the plant, this factor of increasing concentration through accumulation is unlikely to retard the absorption of ions from the soil. Especially is this true of nitrate and ammonium ions, which are utilised in the synthesis of protein.

Several theories have been advanced to account for the absorption of ions by roots, in addition to that achieved by simple diffusions into 'free space'. One of these, elaborated by Lundegärdh and subsequently modified by Robertson, has an electro-chemical basis. It suggests that cytochrome (page 433) in the oxidised state, containing one atom of ferric iron per molecule, is present at the surface of root cells. On to these molecules of oxidised cytochrome negative ions are adsorbed. By random movement of this composite body the ion could be transferred to an adjacent cytochrome centre, a little removed from the root hair surface. This stepwise activity could be continued, involving the transfer of the ion from centre to centre, until eventually the inner surface of the plasma membrane (page 304) is reached, where the iron of the cytochrome centre concerned is converted to the ferrous state. Accordingly the negative ion is released and the whole cycle may be repeated con-

tinuously. The accompanying diagram, modified from Lundegärdh in *S.E.B. Symposium* 8, 1954, will serve to illustrate the mechanism. Positive ions are possibly adsorbed on to acid radicles in exchange for hydrogen ions, being then passively transported along the electrical gradient created by the absorption of negative ions, thus maintaining neutrality. Just as cytochrome may be responsible for the active migration of negative ions and the passive transport of positive ions, so proteins of the plasma membranes may possibly facilitate the active migration of positive ions and the passive transport of negative ones. Thus the two ions of a mineral salt are not necessarily absorbed at the same rate, always

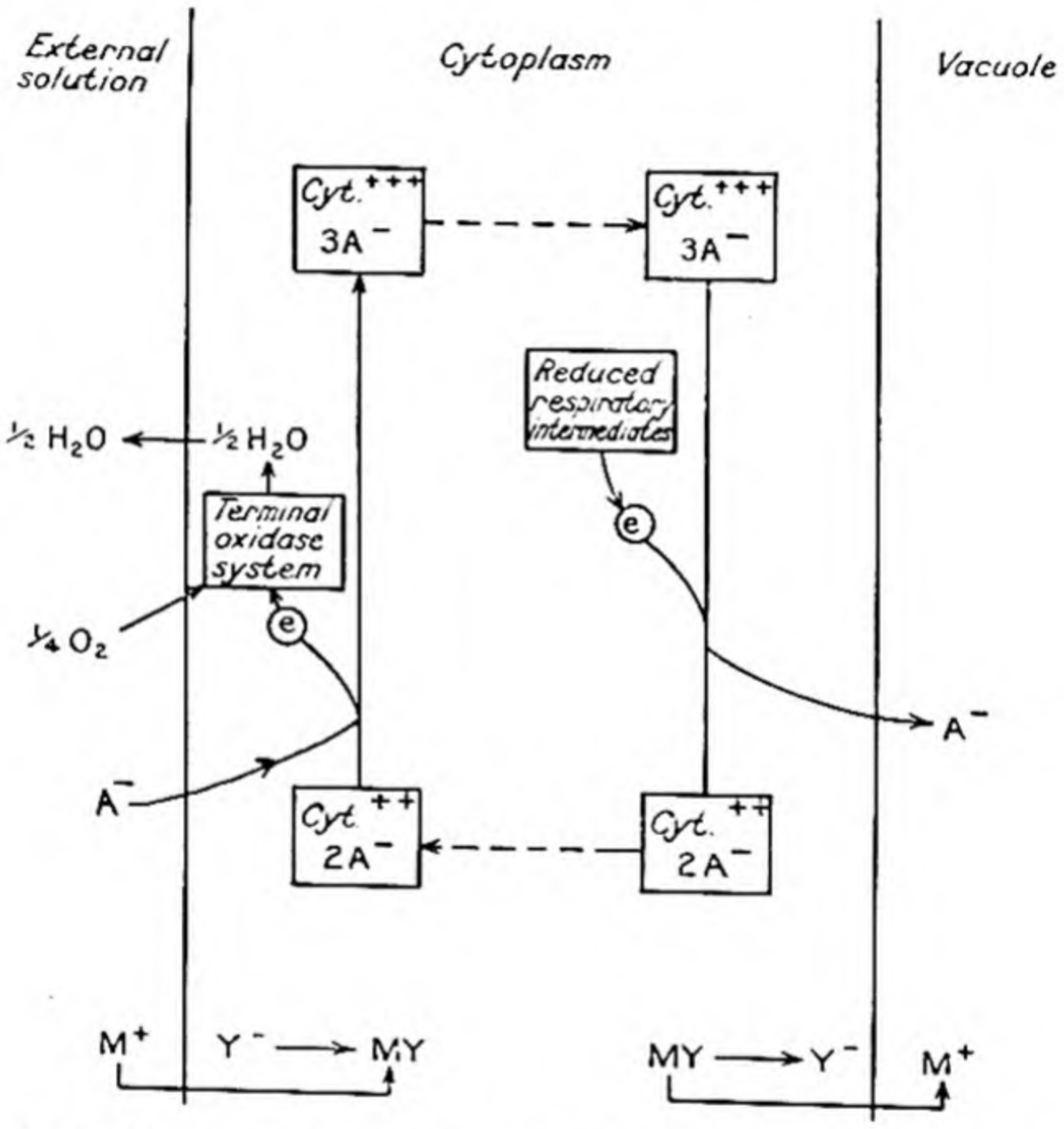


FIG. 245 – Diagram to represent the Lundegärdh hypothesis of salt absorption. (Modified from Lundegärdh in *S.E.B. Symposium* 8, 1954.)

assuming that there are compensatory movements of ions – e.g. H^+ or $(HCO_3)^-$ – from the root to the external medium.

But selectivity of absorption still remains unaccounted for. Some plants, for example, absorb potassium more readily than sodium ions, though both are univalent. It is well known that many complex phospho-

compounds have a greater affinity for potassium than for sodium. Ions may be adsorbed at cell-surfaces on to these complex molecules, only to be released again within the cell when the phospho-compounds, which are acting as carriers, themselves become involved in protein synthesis. Phosphate ions are themselves caused to combine with some as yet unidentified carrier substance to form such compounds as adenosine triphosphate, subsequently being released within the protoplast. Thus selectivity of absorption may ultimately be satisfactorily explained on a chemical basis.

Goldacre and Lorch have suggested that fluctuations in the shapes of protein molecules may provide a mechanism for the absorption of ions. At the cell-surface the molecules are expanded and ions are adsorbed on to the side-chains. Transport across the plasma membranes occurs as the molecules contract, whilst at the inner surfaces of the membranes the ions are released when the side-chains become involved in cross-linkages as the molecules bend.

To explain conduction of salts across the cortex of the root and ultimately to the xylem it is suggested that the protoplasts of the separate cells are combined in a single living unit – a *symplast* – since individual protoplasts are connected together through pores in the cell-walls. Thus the ions may be transported from soil to xylem by a combination of the above mechanisms. The cell-vacuoles may act as reservoirs for ions, some of which leak into them temporarily, only to resume their journey towards the xylem later.

For further reading on this subject the student is referred to an article by J. F. Sutcliffe in *Science News*, No. 25, published by Penguin Books.

PRACTICAL WORK

Chemical Tests for Foods

CARBOHYDRATES. Make stock solutions of glucose and sucrose (a boiling-tube full of each). Make a suspension of starch by smashing up small pieces of raw potato in a little water. With these preparations perform the following tests.

I. *All preparations.* To each in turn add a few drops of 3% alcoholic thymol and an excess of concentrated hydrochloric acid. Boil for a few minutes, with repeated shaking. A carmine coloration results. This test is suitable even for carbohydrates insoluble in water, since they dissolve in the hydrochloric acid.

II. *Glucose and sucrose.* Add about 3 c.c. of concentrated nitric acid and a few drops of dilute potassium chromate solution. A blue coloration results.

III. *Glucose only* (*a*) Add a small quantity of sodium hydroxide and warm. A brown colour appears.

(*b*) Trommer's test. Add two drops of dilute copper sulphate and then sufficient sodium hydroxide solution to redissolve the precipitate of copper hydroxide formed. Warm gently, when an orange-red precipitate of cuprous oxide is formed.

(*c*) Fehling's test. Add an equal volume of Fehling's solution and boil. An orange-red precipitate of cuprous oxide results.

(*d*) Benedict's test. Add a few drops of Benedict's solution and boil. On cooling a yellow or orange precipitate appears, depending on the amount of sugar present.

(*e*) Make the solution alkaline with a little sodium hydroxide solution and add a few drops of methylene-blue. Boil, and the colour disappears.

(*f*) Add ammonium hydroxide to a solution of silver nitrate and pour in a few drops of the glucose solution. Warm gently. A silver mirror is deposited on the sides of the test-tube.

(*g*) Osazone test. To 10 c.c. of a 2% glucose solution add 1 c.c. of glacial acetic acid, as much phenyl hydrazine hydrochloride as will lie on a sixpence, and at least twice this amount of solid sodium acetate. Warm slightly, mix thoroughly and filter into a clean tube. Place this tube in a water-bath and boil continuously for thirty minutes. Then cool slowly. A yellow crystalline precipitate will appear, and a small portion of it should be examined microscopically, when it will be observed that the needle-shaped crystals characteristically arrange themselves in fan shaped clusters or crosses.

Attempt some of tests III (*a*) to (*g*) with the sucrose solution and the starch suspension and notice that they give no positive results. They are, in fact, tests for reducing sugars only. To the sucrose solution add a few drops of concentrated hydrochloric acid and boil for a few minutes. Cool, and neutralise with caustic soda solution. It will be found that this solution now responds to tests III (*a*) to (*g*), since hydrolysis has been effected.

PROTEINS. Make a protein solution by shaking up egg albumen with twenty times its own volume of water, adding a little common salt. With this solution perform the following tests.

(*a*) Biuret Test. Add about 5 c.c. of caustic soda solution to about the same quantity of protein solution. To this add a very few drops of dilute (1%) copper sulphate solution. A violet coloration results.

(*b*) Arginine Test. Make a little protein solution alkaline with caustic soda, and add five drops of 2% α-naphthol solution in alcohol and then five drops of sodium hypochlorite solution. A carmine coloration appears.

(*c*) Xantho-Proteic Test. Add a few drops of concentrated nitric acid to the solution, and a white precipitate is formed. Boil this, when it turns

yellow. Cool and carefully make alkaline with ammonium hydroxide; the precipitate becomes orange in colour.

(*d*) Millon's Test. Add Millon's reagent to the solution. A white precipitate is formed, which goes red on heating.

(*e*) Sulphur Test. Add a few drops of lead acetate solution and sufficient caustic soda solution just to redissolve the precipitate of lead hydroxide first formed. Boil the mixture. The presence of sulphur in the protein is indicated by the appearance of a dark brown solution, owing to the formation of lead sulphide.

FATS. For the following test for fats olive oil is suitable.

Shake up a small quantity of olive oil with an equal volume of sodium hydroxide solution in a test-tube. Immerse the whole in a bath of boiling water for about half an hour. Remove the tube and notice that the contents separate out into three layers. The bottom layer is unchanged alkali and glycerol, the latter being formed by the hydrolysis of the fat. Above this there is formed on cooling a solid soap – the sodium salt of the fatty acid liberated. Floating on the surface is unchanged oil. Remove the three layers into separate tubes. Wash the soap in cold water and then dissolve it by boiling in water. Add a few drops of hydrochloric acid, when the fatty acid is liberated as a white precipitate. To the suspected glycerol add a few drops of 5% potassium chromate solution, followed by an excess of nitric acid. A blue coloration results.

Analysis of Plant Ash

Chop some leaves into small pieces and heat for some hours in a crucible, regulating the flame so that the crucible just fails to glow. After a while a white, powdery residue remains. During the heating the carbon is eliminated as carbon dioxide, the hydrogen as water, and most of the nitrogen as the element itself. A number of components of the ash may be readily tested for.

(*a*) *Sodium.* Clean a platinum wire with concentrated hydrochloric acid and test the ash. A yellow flame indicates the presence of sodium.

(*b*) *Potassium.* This may be detected by a flame test if blue glass is interposed to mask the yellow of the sodium.

(*c*) *Sulphur.* Boil the ash with a small quantity of water. Filter, acidify the filtrate and add barium chloride solution. A white precipitate indicates the presence of sulphur as a sulphate.

(*d*) *Phosphorus.* Prepare a filtrate as in (*c*) and add an equal volume of nitric acid. Add an excess of ammonium molybdate solution and boil. A yellow precipitate shows the presence of phosphates.

Water Cultures

Prepare a number of solutions according to the following instructions:

(*a*) Calcium nitrate 4 grams, potassium phosphate (KH_2PO_4) 1 gram;

potassium nitrate 1 gram; magnesium sulphate 1 gram. Dissolve in 50 c.cs. of distilled water. This solution is complete.

(*b*) As above but with calcium sulphate instead of calcium nitrate and potassium chloride instead of potassium nitrate. In this solution there are no nitrate ions.

(*c*) As (*a*), but without potassium phosphate. Thus no phosphate ions are present.

(*d*) As (*a*), but with potassium phosphate and nitrate replaced by the corresponding sodium salts. There are then no potassium ions present.

(*e*) As (*a*), but omit calcium nitrate, so that there are now no calcium ions.

For the making of solutions for the following experiment use about 1.5 c.cs. of the stock solutions to 500 c.cs. of distilled water. Add two drops of ferric chloride solution.

Thoroughly sterilise five small gas jars by washing successively with concentrated nitric acid, distilled water, mercuric chloride and boiling distilled water. In this case experimental plants may be prevented from becoming diseased. As an additional precaution the culture solutions should each be boiled for about an hour, the loss due to evaporation being made up with distilled water. Each jar is then filled with one of the culture solutions and clearly labelled after being covered with brown paper.

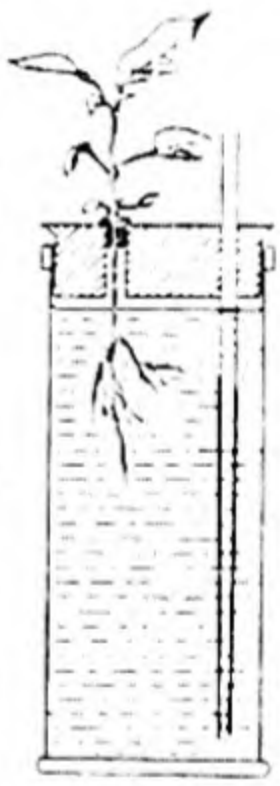


FIG. 246 – Apparatus used for water culture experiments.

Germinate selected seeds, wallflowers being suitable for the purpose. When the seedlings are well developed insert one through a hole in a cork placed in the mouth of each gas jar. If necessary fix them in position with asbestos fibre. Through another hole in the cork insert a glass tube. This permits of the entrance of air to the roots, as well as facilitating the introduction of additional culture solution when necessary. Observe closely the resultant growth of the seedlings, thereby discovering the significance of the nitrate, phosphate, potassium and calcium ions. If magnesium or iron salts are omitted the plant fails to develop chlorophyll, the leaves becoming pale in colour. In this condition it is said to be *chlorotic*: it dies prematurely.

Transpiration

Two experiments may be performed.

(*a*) TO DEMONSTRATE. Cover a pot containing a leafy plant with tinfoil sufficiently closely to prevent any evaporation. The surface of the soil must be similarly protected. The plant is then placed in warm sunlight beneath a bell-jar. After a while drops of water collect on the bell-

jar. That these are water may be proved by the addition of anhydrous copper sulphate, which is turned blue.

(*b*) TO MEASURE. Construct the apparatus shown in Fig. 247. The stoppers must be of rubber, and not cork, whilst all the joints must be thoroughly greased. As water is given off from the leaves of the plant more is drawn in from the Woulff's bottle to replace it. This, in its turn,

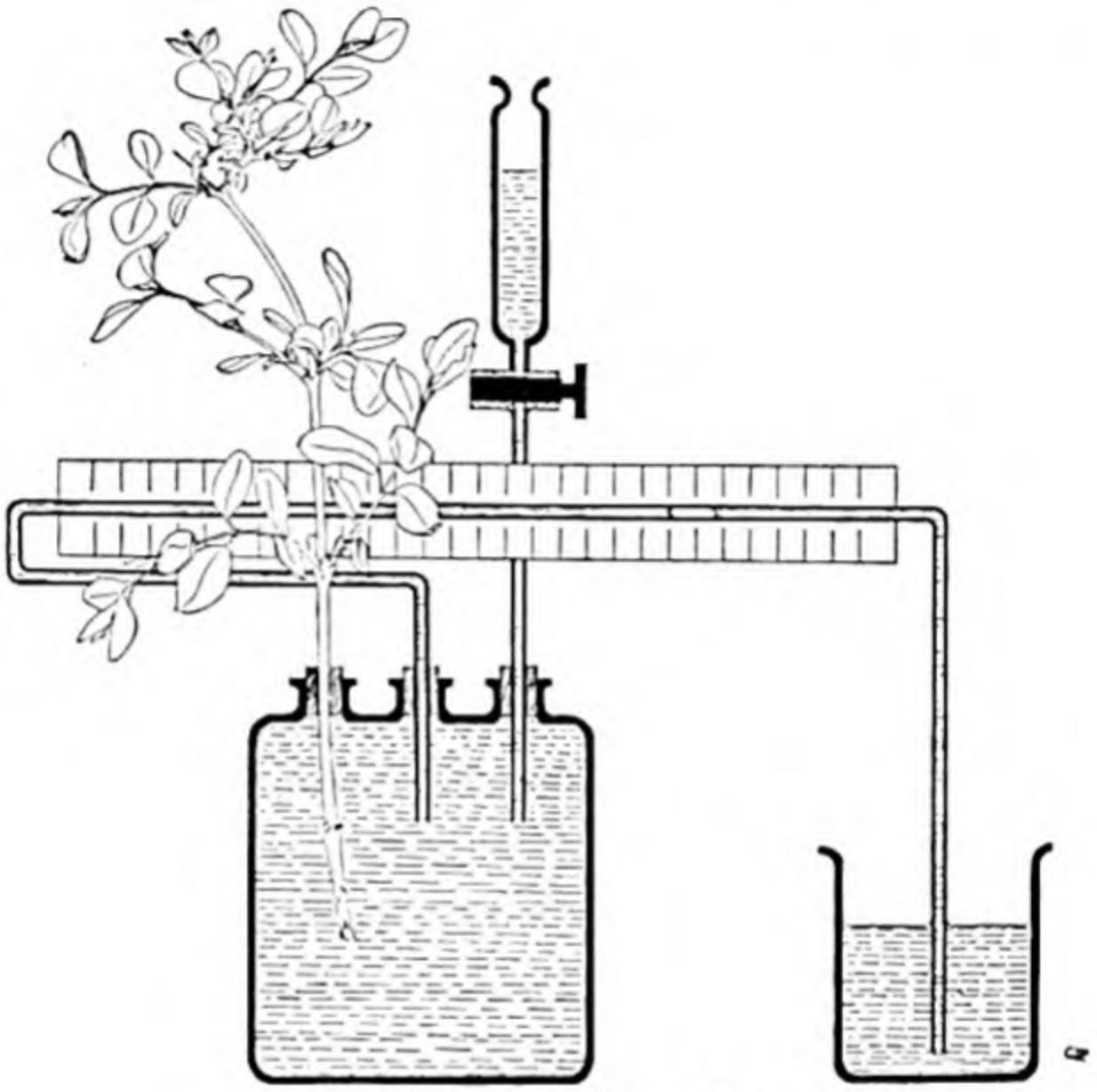


FIG. 247 – Potometer.

results in the withdrawal of water from the narrow tube, so that the air-bubble moves towards the Woulff's bottle. By measuring the distances moved in a given time by the bubble with the apparatus placed in various physical conditions (e.g. light, darkness) the relative rates of transpiration may be ascertained. Such a piece of apparatus is termed a **potometer.**

CHAPTER 23

Nutrition *(continued)*

Once thus within the body of the living organism the food, constituting the raw material, must be converted into body-substance and incorporated into the tissues of the animal or plant. The way in which this is effected will be considered first for animals.

Digestion

The first stage in the conversion of food into the protoplasm of the animal is its partial breaking down into simpler compounds. This is effected by juices produced by the animal, and is termed digestion. It may be seen at its simplest in such lowly forms as *Amoeba*, which engulfs its food, afterwards circulating it through its body. During this process it comes into contact with juices produced by the protoplasm, and is converted into a form which the animal can assimilate, the residual waste being cast out through the ectoplasm. But in higher forms the process of digestion is confined to specialised organs, whilst the food is passed through an alimentary canal, prior to absorption into the blood. It is necessary, therefore, to consider the way in which the various classes of food are dealt with in *Oryctolagus* before the full significance of digestion can be understood.

ENZYMES. In the first place it is observed that the actual quantity of various juices formed is quite inadequate for them to react in a purely chemical manner upon the food. They do, in fact, contain substances in the nature of catalysts, though they differ in a few respects from the ordinary inorganic catalyst. These substances are known as **enzymes**. They are biological catalysts in that they are produced only by living organisms, whilst they are also colloidal. They are highly specific in the reactions which they catalyse, that is to say they will exert their effect on one type of chemical substance only and invariably yield the same end-product or products. Metallic catalysts, on the other hand, may be used to hasten many unrelated inorganic, and even organic, reactions. Enzymes are highly sensitive to temperature-change, being completely inactivated by a few minutes' boiling. They are also very largely controlled by hydrogen ion concentration, being active only within certain narrow limits. Fundamentally all digestion is a process of **hydrolysis** – i.e., chemical combination of the food with water – the enzymes merely accelerating the reactions. In the vertebrates these enzymes make their appearance in very definite parts of the alimentary canal, and their distri-

bution and mode of action may best be followed by means of a detailed study of the process of digestion in *Oryctolagus*.

MAMMALIAN DIGESTION. The food is first chewed in the mouth, thus greatly increasing its surface-area. In the mouth the food encounters **saliva**, produced by four pairs of glands. These are the sub-maxillary, the infraorbital, the parotid and the sublingual. In most mammals, though not in the rabbit, this juice contains an enzyme, known as *amylase*, which assists in the digestion of starch and glycogen, converting them to maltose ($C_{12}H_{22}O_{11}$). The food is then rolled by the tongue into pellets, passing along the oesophagus into the stomach. Here it encounters **gastric juice** and **hydrochloric acid**, both produced by gland-cells lining the stomach. The gastric juice contains two enzymes – *pepsin* and *rennin*. The former assists in the conversion of proteins to peptides. It is actually liberated from the lining cells of the stomach in the form of an inactive precursor, known as *pepsinogen*. This is converted into the active pepsin by the hydrochloric acid, which thus functions as an activator, or coenzyme. Once this reaction has begun, the presence of free pepsin is also responsible for the continued conversion of pepsinogen into pepsin. This phenomenon is termed *autocatalysis*, since pepsin is acting as a catalyst in the formation of more pepsin. Rennin curdles milk, converting its soluble caseinogen into insoluble casein. This is important in the young animal, fed on milk by the mother, since curdling causes the milk to be retained longer in the stomach, and thus more fully acted upon by the pepsin. The hydrochloric acid reaches a strength up to $\frac{N.}{10}$ It is essential for the action of pepsin, as well as which it effects the hydrolysis of maltose and surcose, according to the equations:

$$\underset{\textit{Sucrose}}{C_{12}H_{22}O_{11}} + H_2O = \underset{\textit{Fructose}}{C_6H_{12}O_6} + \underset{\textit{Glucose}}{C_6H_{12}O_6}$$

$$\underset{\textit{Maltose}}{C_{12}H_{22}O_{11}} + H_2O = \underset{\textit{Glucose}}{2C_6H_{12}O_6}$$

The acid also stops salivary digestion and regulates the opening and closure of the pyloric sphincter muscle. It functions also as an internal antiseptic, destroying any noxious Bacteria which may enter with the food. A certain quantity of *lipase* (see later) is also present in the gastric juice, but unless the fats have been previously (artificially) emulsified it is unable to effect any active digestion.

In the duodenum the food meets first the **bile** and then the **pancreatic juice**. The bile itself is usually green in colour, due to the presence of *biliverdin*, a decomposition product of haemoglobin. In man it is golden yellow, since it contains *bilirubin*. There are present also lecithin and cholesterol ($C_{27}H_{45}OH$), a lipoid somewhat similar to ergosterol

($C_{27}H_{41}OH$), the precursor of vitamin D. It contains a small quantity of sodium chloride and sodium bicarbonate, the significance of which will be dealt with subsequently. The bile serves to emulsify fats, breaking them up into small globules as a result of the reduction of their surface-tension. This action is largely facilitated by the presence of bile salts, which are salts of acids closely related to cholesterol. In man the main ones are sodium taurocholate and sodium glycocholate. Owing to its alkaline nature bile stops the action of the gastric juice. The pancreatic juice contains three enzymes. *Amylase*, similar to that found in the saliva, aids in the conversion of starch and glycogen into maltose. *Lipase* converts fats into fatty acids and glycerol. The third pancreatic enzyme is *trypsin*, but it is actually secreted in the form of an inactive precursor, known as *trypsinogen*. In the small intestine this encounters an activator, or coenzyme, known as *enterokinase*. The result is that the trypsinogen is converted into trypsin. Nor is this all. There is, in fact, in pancreatic juice, a second precursor, known as *chymotrypsinogen*. The presence of trypsin is responsible for the conversion of this, in the small intestine, into active *chymotrypsin*, similar in function to the trypsin. Furthermore, the actual presence of trypsin in the small intestine is responsible for the further conversion of trypsinogen into trypsin. This is a further case of autocatalysis. It will be remembered that the bile is alkaline, owing to the presence of sodium bicarbonate. This serves partially to neutralise the acidity of the food entering from the stomach, but the *p*H value of the duodenal contents remain between 4.5 and 5.1.

The food now passes into the intestine, where it meets a final digestive juice, the **succus entericus**, which contains a number of enzymes. *Erepsin* promotes the conversion of peptides to amino-acids, whilst *sucrase* accelerates the inversion (hydrolysis) of sucrose to glucose and fructose. Thus –

$$\underset{\textit{Sucrose}}{C_{12}H_{22}O_{11}} + H_2O \rightleftharpoons \underset{\textit{Glucose}}{C_6H_{12}O_6} + \underset{\textit{Fructose}}{C_6H_{12}O_6}$$

Maltase and *lactase* catalyse the hydrolysis of maltose and lactose respectively, the former becoming converted into glucose and the latter into glucose and galactose. The table on page 392 may be useful as a summary of the information gleaned concerning the digestive juices.

In conclusion reference must be made to a totally different means whereby digestion is effected. There are found in the caecum of the rabbit certain Protozoa and Bacteria, capable of digesting cellulose, which forms the bulk of the rabbit's food. This cellulose is thus rendered available to the animal, in return for which service the inhabitants receive supplies of nitrogenous food. This is, then, a case of symbiosis between animal and plant (page 669).

The passage of the food along the alimentary canal is facilitated by a wave of muscular contraction passing in the direction of the anus, just as

Substrate	Part of gut	Juice	Enzyme	End-product
Starch and glycogen	Mouth	Saliva	Amylase*	Maltose
	Duodenum	Pancreatic	Amylase	Maltose
Maltose	Stomach	Hydrochloric acid	H•ions[1]	Glucose
	Duodenum	Pancreatic	Maltase	Glucose
	Intestine	Succus entericus	Maltase	Glucose
Sucrose	Intestine	Succus entericus	Sucrase	Glucose and fructose
Lactose	Intestine	Succus entericus	Lactase	Glucose and galactose
Proteins	Stomach	Gastric	Pepsin	Peptides
	Duodenum	Pancreatic	Trypsinogen+	
	Intestine	Succus entericus	Enterokinase (= Trypsin)	Peptides
Peptides	Duodenum	Pancreatic	Erepsin	Amino-acids
	Intestine	Succus entericus	Erepsin	Amino-acids
Fats	Duodenum	Bile		Emulsified fat
	Duodenum	Pancreatic	Lipase	Glycerol and fatty acids
Mineral salts	Stomach	Hydrochloric acid		Soluble chlorides
Caseinogen	Stomach	Gastric	Rennin	Casein

[1] The H• ions are not, of course, true enzymes, but here they act catalytically.
* There is no salivary amylase present in the rabbit.

an object within a rubber tube may be forced along by passage of the thumb and finger. This movement in the animal is known as *peristalsis*.

DIGESTION IN OTHER ANIMALS. In principle the digestive process is similar in all forms where an alimentary canal is developed, though in lower forms it is, as would be expected, less highly organised. Thus in *Lumbricus* the oesophageal glands produce calcium carbonate, which is passed from the oesophageal pouches into the lumen of the gut, where it neutralises acids entering with the food, and this is probably important for allowing digestion to occur. The inner wall of the intestine produces digestive juices, the specific enzymes of which are not properly known. The salivary glands and the hepatic caeca of the cockroach elaborate digestive juices which are passed into the gut. It is important to notice

that there is no saliva present in fish or Amphibia. This condition would be expected in fish, since the respiratory process involves the passage of a continuous stream of water through the mouth, so that any saliva formed would be carried away. In the frog rennin is absent from the gastric juice, whilst the enzymes of the succus entericus are fewer in number.

Absorption and Distribution

The purpose of digestion is to render the food both soluble and assimilable. Absorption then takes place as the food passes through the later portion of the gut – e.g. the intestine of vertebrates. It is not sufficient for the food merely to be soluble: the molecules must be of such a size that they can pass through the membrane provided by the endothelium of the intestine. Sucrose, for example, is soluble, but before it can be absorbed

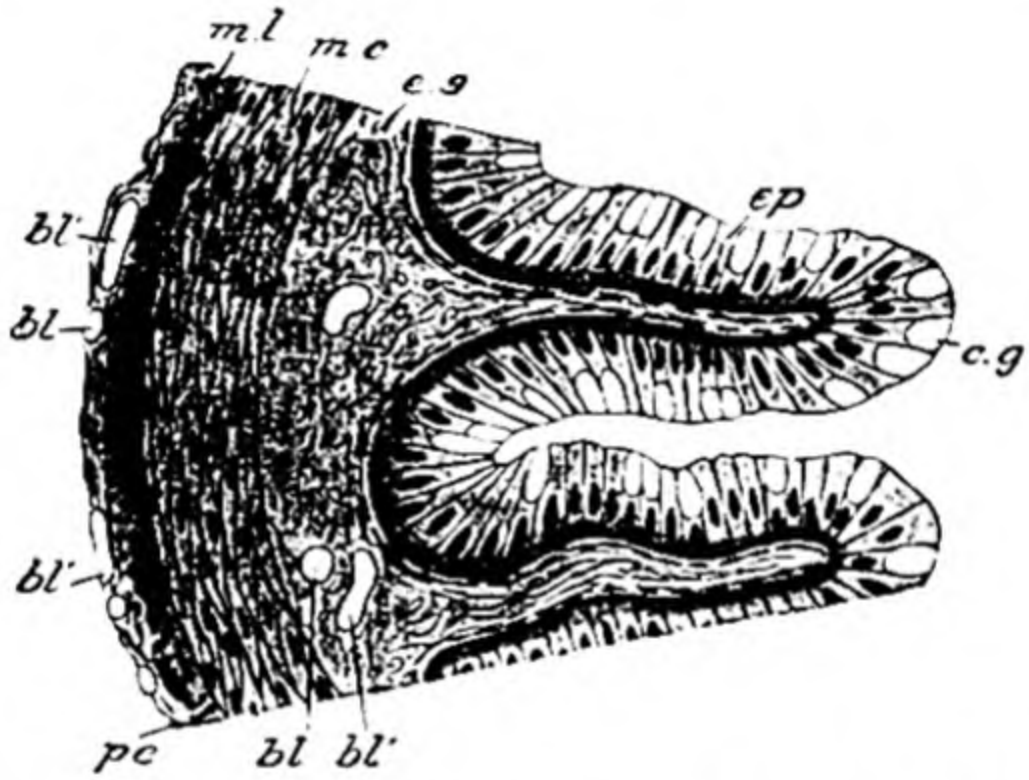


FIG. 248 – *Rana*. Portion of a transverse section of the intestine. (From 'Atlas of Practical Elementary Zootomy', by G. B. Howes. Macmillan.)
bl., artery; *bl'.*, vein; *c.g.*, mucous globule; *ep.*, epithelial lining; *e.s.*, connective-tissue layer; *m.c.*, circular muscular layer; *m.l.*, longitudinal muscular layer; *pc.*, peritoneum.

it must be hydrolysed to form glucose and fructose. To facilitate this absorption the surface of the intestine is beset with a vast number of finger-like projections, each of which is termed a **villus**. Running in each villus is an artery and a vein, as well as a lacteal for the carrying away of fatty materials. Some fat is resynthesised in the cells lining the lacteals. The detailed structure of the wall of the stomach and intestine is described on page 341. The typhlosole of *Lumbricus* and the spiral valve of *Scyliorhinus* also serve to increase the surface-area of the intestine. Once thus absorbed into the blood the food is distributed to all parts of the body. A large amount of the carbohydrate material of vertebrates is stored in

the liver in the form of glycogen, whilst glucose provides the chief carbohydrate currency.

In certain animals these later stages are somewhat modified according to circumstances. Thus in *Hydra* the food absorbed and ingested by the endoderm cells lining the coelenteron needs merely to diffuse into the cells of the ectoderm, whilst in *Obelia* the same is true for the individual hydranths, though the blastostyles receive their food via the hydrocaulus. In the majority of internal parasites there is no mouth or alimentary canal, the food being absorbed ready digested from the host. This condition is seen in *Taenia*.

Assimilation

The ultimate result of nutrition is the production of new protoplasm or the supply of fuel to the working organs. The former primarily involves the condensation of amino-acids into the diagnostic protein of the animal concerned. These proteins are characteristic of both the species and the tissues, and much attention has been devoted recently to the mechanism by which this specificity is possibly achieved. What might be termed the 'template' hypothesis has emerged, comparable with the metal master template from which innumerable plastic discs of one piece of recorded music may be manufactured. But what is the living template within the cell? Desoxyribonucleic acid, known as *DNA* (page 313) and localised on the chromosomes, has been nominated for this role. That it is operative has been proved in experiments using bacteria, for it is found that if one species is exposed to a solution of *DNA* derived from another, then the treated species will proceed to synthesise a different type of protein. But it would appear unlikely that the control of *DNA* over protein synthesis is as direct as that of the template over the manufacture of plastic discs, for recently it has been shown that artificial removal of nuclei from cells does not destroy their ability to synthesise protein. It would also appear to be generally true that cells rich in the similar, but not identical, ribonucleic acid (*RNA*) possess the greatest capacity for synthesising protein. Since the microsomal fraction (page 303) of the cytopolasmic inclusions contains most of the *RNA*, it is here that protein synthesis mainly occurs. It would seem likely, therefore, that *DNA* acts as the architect of protein synthesis, passing instructions to *RNA*, which assumes the role of the contractor on the job. Realising that the location of *DNA* is on the chromosomes, it would appear that the specific characteristics of an organism are, in fact, a reflexion of its protein structure. The method by which *DNA* exerts its control, through *RNA*, is still obscure.

The synthesis of new protoplasm necessarily requires energy, the source of which is mainly the carbohydrate and fat content of the food, whilst the synthesis itself may result either in growth or in the replacement of tissues in compensation for wear and tear.

The nutrition of green plants is very different from that of animals.

The process of digestion is essentially one of partial analysis, for the compounds taken in as food are reduced in complexity prior to absorption. But in plants the bulk of the nutritive process is synthetic, and the first stage is the one of primary importance.

Photosynthesis

Broadly speaking, photosynthesis is the conversion of water and carbon dioxide into sugars, accompanied by the evolution of oxygen. It takes place in the presence of sunlight, and is facilitated by the chlorophyll in the assimilating tissues. There are, however, several points to be considered in greater detail.

PROPERTIES OF CHLOROPHYLL. Owing to the importance of chlorophyll in the process of photosynthesis it is now necessary to get some idea of its chemical and physical nature. It is a composite pigment, consisting of chlorophyll *a* ($C_{55}H_{72}O_5N_4Mg$), chlorophyll *b* ($C_{55}H_{70}O_6N_4Mg$), carotenes (e.g., $C_{40}H_{56}$) and their oxygen-derivatives, known as carotenoids (e.g., $C_{40}H_{56}O_2$). Their chemical formulae give some indication of their complexity. Chlorophylls *a* and *b* are both

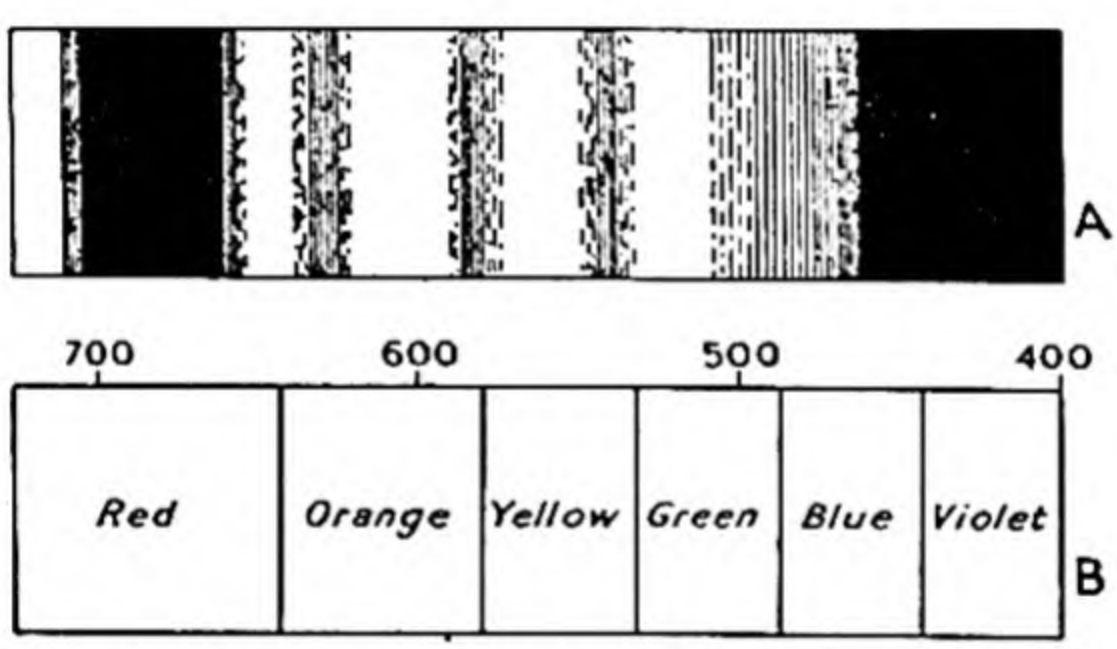


FIG. 249 – Diagram to show the absorption bands produced in the spectrum as a result of the passage of light through a colloidal solution of chlorophyll. Figures above B indicate wave-length.

green, whilst carotenes are orange-red and carotenoids yellow. Chlorophyll is present in well-defined bodies, termed **chloroplasts**. These have been extremely constant in structure over vast evolutionary periods, though variable amongst the Algae. In all higher plants (from the Bryophyta upwards) they are biconvex discs, containing chlorophyll. Each is a protoplasmic body, of gel consistency, bounded by a semi-permeable membrane. It consists of a colourless base, termed the **stroma**, in which are distributed particles, known as **grana**, which contain the chlorophyll in association with protein and lipoid materials. The grana take the form of piles of submicroscopic lamellae, composed of macromolecular films, thus allowing a high rate of energy exchange. In some cases the grana

may be quite large. Thus, in mosses, for example, they actually impart a mottled appearance to the chloroplasts. Plastids are developed from bodies termed *pro-plastids*, which are derived ultimately from the oösphere, where they resemble mitochondria. If light is allowed to pass through a solution of chlorophyll and is then analysed by a prism it is

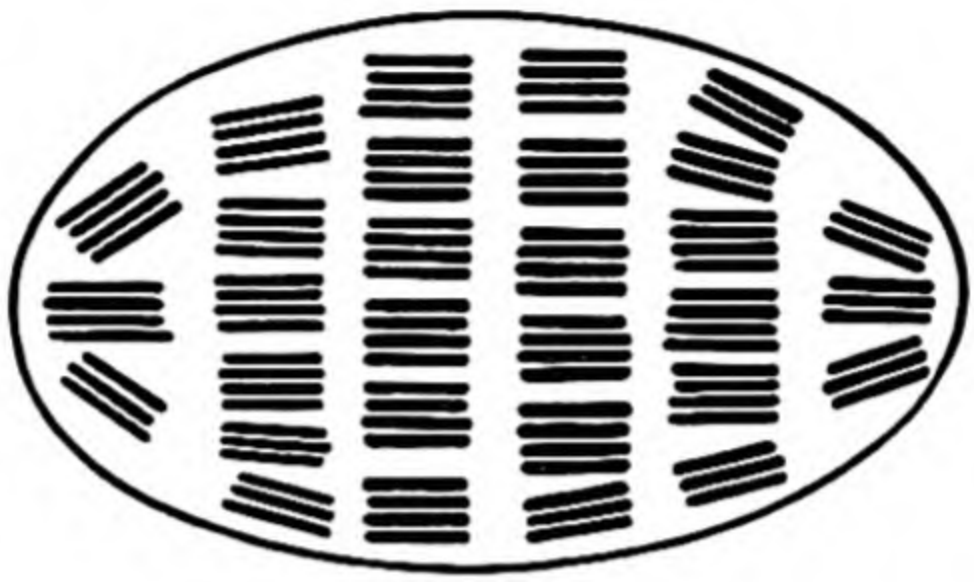


FIG. 250 – Diagram to represent the arrangement of grana in a chloroplast. (After Frey-Wyssling.)

seen that certain colours are missing from the normal spectrum, as shown in Fig. 249A. It is presumable, therefore, that red and blue lights are active in effecting photosynthesis. Actually blue is least effective and red most, whilst green and yellow occupy intermediate positions. But only part of the total process is influenced by light, since it has been shown that, in the presence of abundance of light and carbon dioxide, the rate of photosynthesis is approximately doubled by a rise in temperature of 10° C (within certain limits). Normally carbon dioxide, whose concentration in the atmosphere is but 0.03%, acts as the limiting factor on the rate of photosynthesis. If this be artificially increased to 0.25% then the intensity of light becomes the limiting factor. In fact a limit can be imposed by temperature only in the presence of much carbon dioxide and not less than 0.69 of full sunlight. The chemical efficiency of the chloroplast has been calculated as about 35%.

MECHANISM OF PHOTOSYNTHESIS. The reactions involved may be summarised by the following general equation –

$$CO_2 + H_2O + \textit{light-energy} \rightarrow \underbrace{(CH_2O) - 112K} + O_2,$$

where (CH_2O) represents, in a conventional and non-committal form, a molecule of carbohydrate. But such a reaction necessarily proceeds through a number of intermediate stages and many theories have been advanced to account for the final result. All earlier hypotheses required

that at least one atom per molecule of evolved oxygen should come from the carbon dioxide participating. In Beyer's hypothesis, for example, the sequence of events suggested was –

(1) $CO_2 \longrightarrow CO + O$, $H_2O \longrightarrow H_2 + O$, $O + O \rightarrow O_2$

(2) $CO + H_2 \rightarrow H.CHO$

Formaldehyde

(3) $6H.CHO \rightarrow C_6H_{12}O_6$

More recently the source of the evolved oxygen has been investigated to determine whether it comes from the water or the carbon dioxide. Ruben *et alia* (1941) used 'heavy' oxygen (O = 18) in known proportions in the water and carbon dioxide used in photosynthesis experiments with *Chlorella*. The emergent oxygen was analysed for its O^{18} content by mass spectrometry and the proportion of O^{18} in the gas was found to be the same as that in the water. It was concluded, therefore, that all the oxygen evolved in photosynthesis comes from the water. Thus the above equation must be modified, so that the simplified version now becomes –

$$CO_2 + 2H_2O + energy \rightarrow (CH_2O) + H_2O + O_2$$

This evidence supports the view of van Niel (1931) that photosynthesis is an oxidation-reduction reaction, involving the oxidation of water and the transfer of its hydrogen to carbon dioxide in reduction. The hydrogen donor need not be water. In the green Sulphur Bacteria, for example, hydrogen sulphide serves to supply reducing power. Thus –

$$CO_2 + 2H_2S + energy \rightarrow (CH_2O) + H_2O + 2S$$

In fact, some photosynthetic Bacteria can use mulecular hydrogen in the process known as *photoreduction*. Thus –

$$CO_2 + 2H_2 \rightarrow (CH_2O) + H_2O$$

Gaffron (1944) showed that some green Algae (e.g. *Scenedesmus*) can become temporarily adapted to the use of molecular hydrogen by certain treatment.

All this evidence suggests that the process of photosynthesis is fundamentally the same over a wide range of autotrophic plants – i.e. it involves the transfer of hydrogen from a suitable donor to carbon dioxide.

Van Niel later suggested that the removal of hydrogen from water is the stage of the process requiring energy from the light absorbed, and that subsequently the hydrogen is transferred stepwise through a donor-acceptor chain ultimately to carbon dioxide. In other words, the entire process is divisible into two phases –

(1) A photochemical phase, involving the *photolysis* of water.

(2) A dark phase, involving hydrogen transfer and carbon dioxide reduction.

There is much evidence to support this view and a few experimental observations will be quoted. Warburg determined the temperature coefficient (Q_{10}) of photosynthesis. At *low* light intensities the $Q_{10} = \sim 1$, showing that the process is independent of temperature, or that light intensity is the limiting factor. At *high* light intensities, $Q_{10} = \sim 2$, showing that the rate of photosynthesis is now independent of light intensity and is limited by a chemical process.

The same investigator also carried out experiments on *Chlorella*. Equal quantities of light were supplied either continuously or divided into a series of flashes. When the light intensity was *high*, flashing light yielded a greater assimilation – i.e. the total light supplied was used with greater efficiency. When the light intensity was *low*, there was no difference between continuous or flashing light. This is because light intensity is limiting the process and the available light is being used to maximum efficiency.

Assuming the operation of light and dark phases, it may be concluded that the chemical (dark) phase is the slower process and thus, when light intensity is high and illumination is continuous, a proportion of the light energy incorporated in the photochemical phase is wasted. If, however, dark periods are provided by dividing the light into flashes, the dark process is given time to utilise the products of the preceding light period.

Hill showed that when a preparation of isolated chloroplasts was illuminated in the presence of certain hydrogen acceptors (e.g. quinone), oxygen was evolved. Carbon dioxide will not serve as a hydrogen acceptor in the 'Hill reaction'. Thus the photolysis of water is proceeding without carbon dioxide reduction.

Calvin subjected *Chlorella* suspension to illumination in a carbon dioxide-free medium. Immediately afterwards, the alga was exposed to carbon dioxide in the dark. Photosynthesis was not prevented by such pre-illumination – i.e. separation in time of the light phase and the carbon dioxide reduction phase.

When chlorophyll absorbs radiant energy it is believed to become energised by the displacement outwards of electrons of some of its component molecules. When these electrons subsequently revert to their original positions a photochemical effect is exerted by the chlorophyll molecules concerned, and an essential stage in photosynthesis is thus accomplished, for these changes harness the energy required for the photolysis of water. Though such actual chemical change has never been actually observed in illuminated chlorophyll, it must be borne in mind that in plant cells the chlorophyll does not occur freely, but in close association with very large fat and protein molecules. The chemical changes referred to may well take place anywhere within this molecular

complex. Thus, with Z and HZ representing chlorophyll –

$$H_2O + Z \rightarrow (OH) + HZ$$

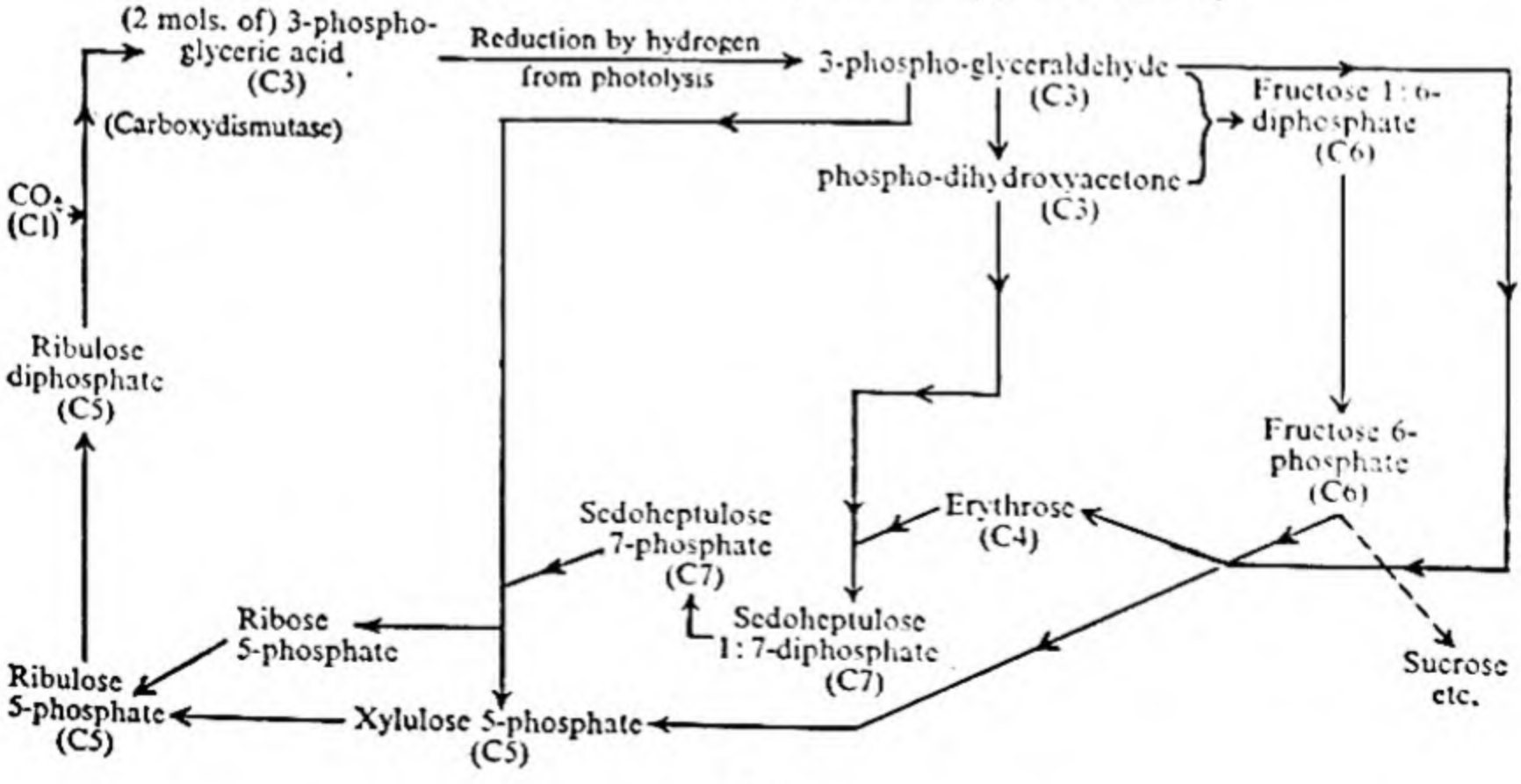
The (OH) portions presumably associate spontaneously in pairs to form peroxides, probably of an organic nature. Thus –

$$2(OH) \rightarrow H_2O_2$$

These peroxides then decompose with the liberation of molecular oxygen.

The production of radioactive isotopes of carbon lent great assistance to the study of photosynthesis. C^{11} (mass number 11) was first used, but its half-life was too short for many purposes. C^{14} is of long half-life and was used by the Calvin group in their classical work which led to a drastic change in ideas of the mechanism of photosynthesis. $C^{14}O_2$ was supplied to *Chlorella* suspension in light. 80% ethanal extracts of cells were prepared and analysed by paper chromatography and radioautography. By reducing the period of exposure to $C^{14}O_2$ to 5 seconds or less, Calvin showed the first product of photosynthesis to be 3-phospho-glyceric acid. This is reduced by the hydrogen from the light reaction to yield 3-phospho-glyceraldehyde. At first, it was believed that the phospho-glyceric acid (*PGA*) was formed by reaction of carbon dioxide with an unknown 'two-carbon acceptor'. Later, however, Calvin discovered that the carbon dioxide acceptor is, in fact, ribulose diphosphate (a pentose phosphate). With carbon dioxide this forms a 6-carbon compound, which splits symmetrically to give two molecules of *PGA*, under the influence of the enzyme, *carboxydismutase*. Some of the *PGA* ultimately yields sucrose, starch, proteins, etc., whilst other enters a cycle for the essential regeneration of the carbon dioxide acceptor, as indicated in the following diagram.

The Carbon Cycle in Photosynthesis (after Calvin).



Protein Synthesis

Whilst a great deal of the carbohydrate material synthesised in a plant is used as a source of energy and for the formation of cell-walls (cellulose is a carbohydrate), a certain amount is utilised in the formation of new protoplasm, involving its conversion into proteins. The essential nature of a protein has already been discussed (page 371). Since proteins are readily formed from amino-acids it is the synthesis of these latter compounds which must be considered. Experimental work has contributed much to the solution of the problems involved, and its principal features will now be considered. It has been discovered that during the daytime the concentration of protein and total nitrogen in green leaves increases, whilst that of nitrates remains low. At night the reverse state of affairs obtains. In the white parts of variegated leaves exposed to light there is much nitrate present, with little or none in the green parts. These results can be accounted for by either of two hypotheses –

(1) Protein is formed from carbohydrates and nitrates.

(2) Protein is formed directly from carbon dioxide, water and nitrates by a modified form of photosynthesis.

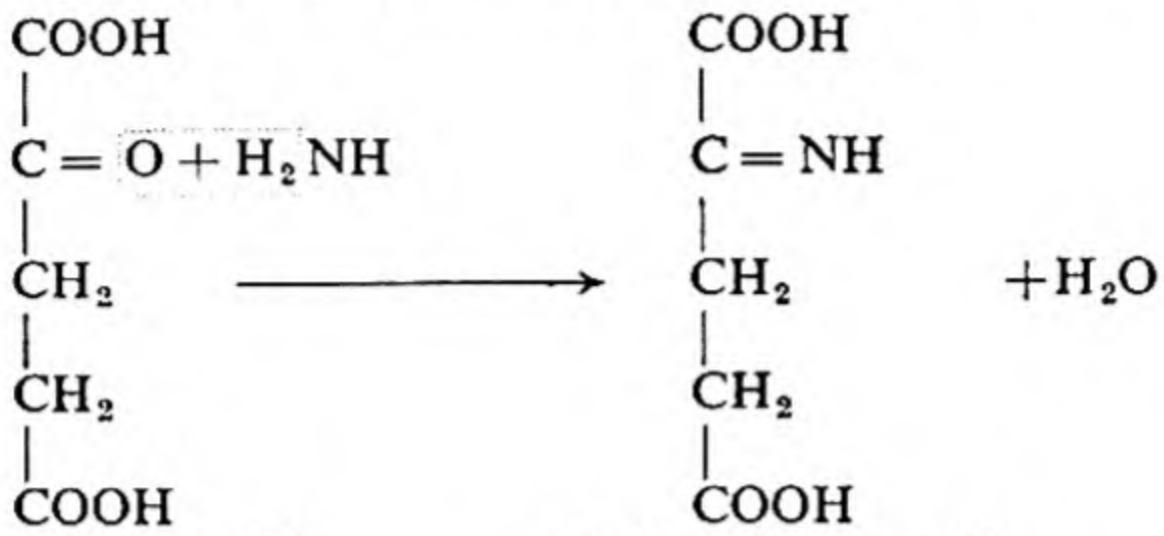
These alternatives have been subjected to experimental test, detached leaves being retained in darkness and supplied with sugars and ammonium salts or nitrates. A significant experiment was performed by Pearsall and Billimoria, using daffodil leaves. They sterilised the surfaces of the leaves with successive applications of calcium hypochlorite and sterile water. Each leaf was then divided into four segments – (*a*) the white meristematic base; (*b*) the yellow-green extending zone; (*c*) the lower green photosynthetic zone and (*d*) the green apex. The segments were then floated on a 0.1 molar phosphate solution at *p*H6, with 3% glucose and 0.3% ammonium nitrate: aeration was adequate and there was presumably enough sulphur present in the sap for the formation of any sulpho-proteins. In zone (*a*) protein synthesis occurred, and to a less extent in zone (*b*): this synthesis was accelerated by light in zone (*b*), but not in zone (*a*). Simpler organic compounds of nitrogen were synthesised. in zones (*c*) and (*d*), especially if the leaves were exposed to light. It would appear from these results that hypothesis (1) is the more likely, and from the fact that proteins are formed in the colourless zone it would appear probable that the sequence of events in a root meristem is similar.

Evidence has been accumulated to suggest that the sequence of events leading to the formation of organic compounds of nitrogen is –

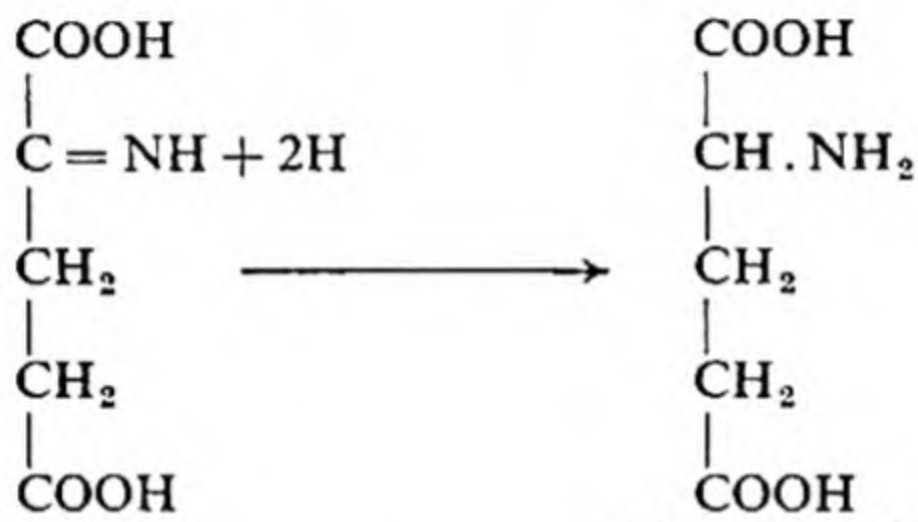
nitrate → nitrite → ammonium salt → amino-compound,

the last named undergoing subsequent condensation. It has been suggested that α-keto acids, derived from sugars, unite with ammonia to form α-imino acids, which, as a result of a reductive process, yield

α-amino acids. The probability of the operation of this sequence has been substantiated by experimenters in Stockholm, who claim to have prepared glutamic acid from ammonia and the corresponding α-keto-glutaric acid. This reaction may have occurred as follows –



α-keto-glutaric acid *α-imino-glutaric acid*



Glutamic acid

It would therefore appear probable that in normal conditions simple nitrogenous organic compounds are synthesised in the green parts of plants, subsequently to be translocated to meristems and storage organs, where final protein assimilation occurs. In adequate supplies of nitrogen salts the rate of formation of these nitrogenous organic compounds is limited by the amount of available carbohydrate – i.e. by the speed of photosynthesis. This would account for the observed relative amounts of organic and inorganic nitrogen to be found in leaves by day and by night, as stated in the early part of this section.

Formation of Fats and Oils

Fats, as already pointed out, are esters of glycerol and the higher fatty acids. Their mode of formation in plants would therefore appear to be as follows. Since sugars are either aldehydes or ketones they will, on oxidation, yield fatty acids. The way in which glycerol is formed is not clear, but it is known to be produced by the fermentation of sugar in alkaline solution. It is not improbable, therefore, that it is formed by enzyme action from sugar in the living plant. The fatty acids and glycerol then unite, with the formation of fats.

Translocation

It is apparent that substances, both inorganic and the simpler organic, are capable of moving from one part of the plant to another, where they may react together or be employed for a particular purpose. Such movement is termed **translocation**. In general, substances move from regions where they are absorbed or formed to regions where they are required. Part of such movement may take place by simple diffusion, whilst the upward stream in the xylem is to some extent facilitated by the transpiration current. Although it is apparent that substances tend to move to all parts of the plant, it is possible for certain definite streams to be recognised. Thus sugars, for example, tend to move away from the leaves, their seat of formation, to stem and root apices and to storage organs. At other times they, together with protein and fatty material, leave the storage organs and travel towards developing buds. In solution in the vessels and tracheids of the xylem have been found not only mineral salts but also sugars and enzymes, and part at least of this stream is believed to be capable of movement in a downward direction. The phloem was for a long time believed to be the principal path of downward movement of carbohydrate and nitrogenous organic material, and this view is now largely re-established after a period of reaction against it. The principal experimenters on this subject are Mason and Maskell and their results are based largely upon 'ringing' experiments, whereby the continuity of the phloem is interrupted. Conduction of carbohydrates takes place only if at least a portion of the phloem is left intact. The same experimental method has been employed to show that food travels upwards in the bark (which includes the phloem) to flowers and fruits. The transport of mobile carbohydrate and nitrogenous materials takes place by a process at least analogous to diffusion along a positive dynamic concentration gradient – i.e. from a region of higher concentration to one of lower. In the cotton plant, for example, the sugars formed in the mesophyll are hexoses. These are mobile and diffuse into the sieve tubes. Here they are mostly converted into sucrose, possibly with the assistance of companion cells. Thus two gradients are preserved – (1) From mesophyll to sieve tubes, since the concentration of hexoses in the mesophyll is maintained by photosynthesis or by the hydrolysis of starch, and (2) Down the sieve tubes, for as sucrose flows away more is formed from the hexoses arriving from the mesophyll.

Much the same consideration may be taken to apply to nitrogenous materials, since the simpler nitrogen compounds are formed principally in the leaves, whereas they may be converted into more complex form in non-green parts of the plant (see page 400).

At this point it is essential to consider in more detail the mechanism involved in translocation. The concept of mass flow, involving a streaming of the solutions concerned along the appropriate channels, as water

may flow through a pipe, was formerly regarded with some favour as the means of distribution of organic substances. It was held to depend upon a difference of turgor between the two ends of the system. There was some evidence in its favour. Thus, a sieve tube punctured by an aphid continues to exude a sucrose solution far in excess in quantity of that contained in such a cell. This suggests a flow through a series of cells, with turgor being destroyed in the damaged one. But difficulties are soon apparent in the way of accepting this hypothesis. Cytological examination does not indicate the presence of sufficiently large connecting channels between consecutive segments of a sieve tube to permit flow at the speed known to be attained. As indicated above, it has been observed that different solutes can move simultaneously at various speeds and even in opposite directions. The alternative hypothesis, maintaining that translocation depends upon the diffusion of solutes along concentration gradients, is not acceptable in its simplest form, for such a phenomenon is inadequate to account for the speed at which various solutes are known to travel, such speeds being demonstrated by the use of suitable isotopes, especially ^{14}C. It is therefore concluded that a form of diffusion in some way activated metabolically by the plant provides the only acceptable explanation. There is much experimental evidence to emphasise the nature of the problem. Labelled amino-acids reach the veins of a rhubarb leaf within a very few minutes of the supply to that leaf of $^{14}CO_2$. Thereafter, the rates at which different amino-acids are translocated are quite different from those at which they are synthesised: they also vary with the stage of growth of the plant. The rate of maintained movement of labelled photosynthetic products is very high, varying from 40 to 120 cm. per hour. This follows an initial rate (in the experimental material) of some 5,000 cm. per hour. An unduly high respiratory rate has been demonstrated in the conducting tissues (xylem, as well as phloem) of sugar beet. In the case of the phloem this may be dependent upon the companion cells, which, together with the sieve tubes, form a single metabolic unit. The products of such oxidations identified suggest that the latter arrive by way of glycolysis and the Krebs cycle. Phosphate bonds are almost certainly involved, since the energy output is so high. That oxidative metabolic processes are involved in the transport of organic substances in plants is further evidenced by the fact that poisons, such as cyanide or carbon monoxide, have a very marked depressent effect upon the speed of such transport.

At present there is no complete answer. It is clear that metabolism within the phloem is involved. But this is not all. It appears that metabolism within the whole plant must be taken into account. Only in this way can the varying directions of distribution or organic material at different stages in the life of the plant be accounted for. Thus, in a very young plant, newly-formed leaves may receive material from more mature leaves and export nothing. Such conduction may occur in the

xylem, into which substances have passed from the phloem. Late in life the general direction of flow changes. Whereas it was formerly towards the roots, it now occurs in favour of developing seeds and fruits, while the roots are virtually starved. For further reading on this topic the student is referred to *Endeavour*, Vol. XX, Number 77 (January 1961), in which is contained a very informative article by Dr A. L. Kursanov.

Even in the xylem conduction is confined to the newer (*sap*) wood, the bulk of the stem consisting of non-conducting *heart* wood.

Mechanism of the Stomata

Now that the process of photosynthesis has been considered in some detail it is possible to appreciate something of the mechanism whereby the opening and closure of the stomata is effected. It will be remembered from the description of the leaf given in Chapter 15 that each stoma is bordered by two guard-cells. It is upon the turgidity, or turgescence, of

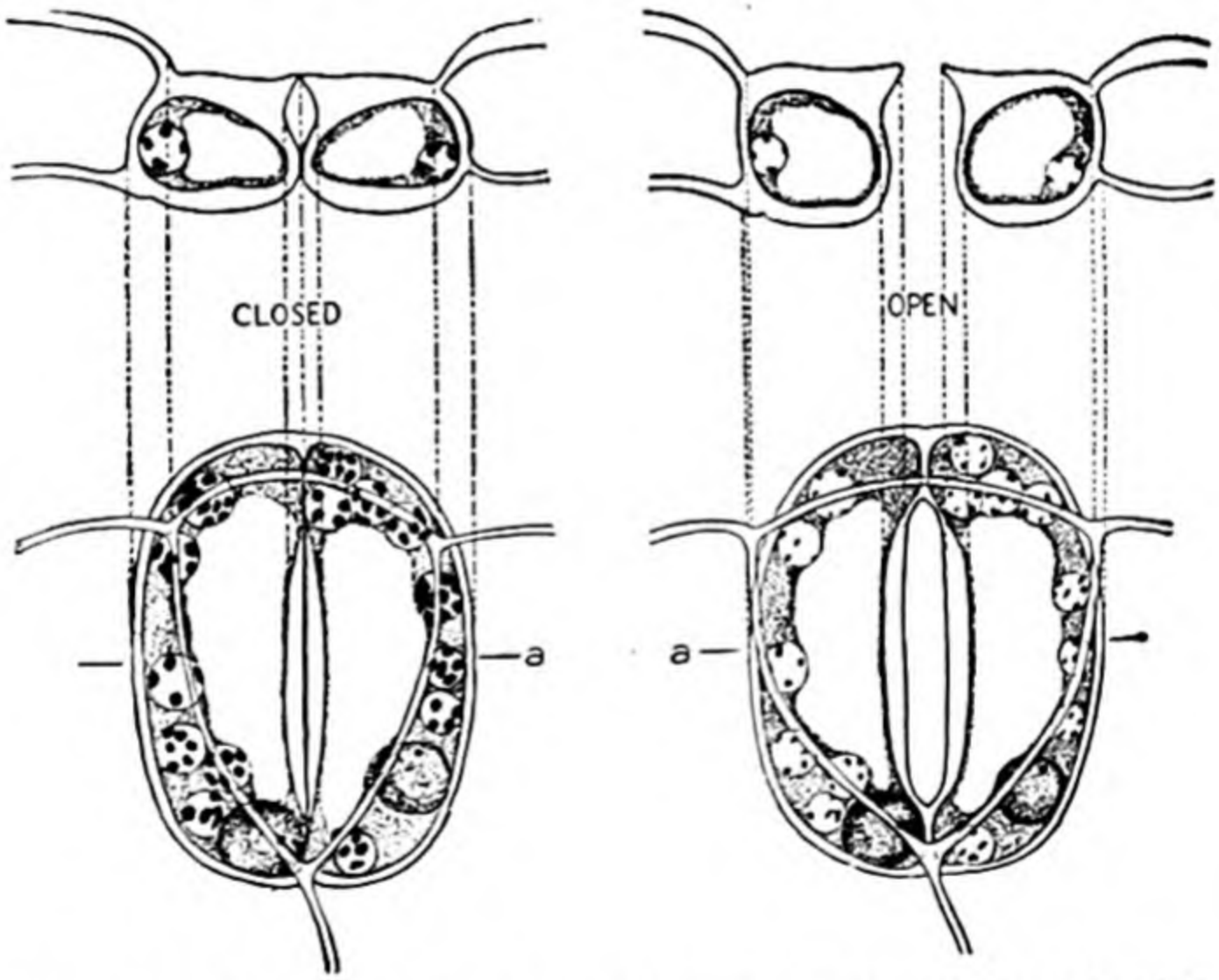


FIG. 251 – Stoma of *Hypericum calycinum*. (From 'An Introduction to Plant Physiology', by W. O. James. The Clarendon Press.) On the left-hand side the stoma is shown closed, and on the right open. Surface views below, with sections along the line *a a* above. Chloroplasts are left white, and their starch grains shown in solid black. Highly magnified.

these cells that the condition of the stoma depends. This in its turn is regulated by the concentration of sugars within the guard-cells, and thus on their suction pressure. When the guard-cells are fully distended their walls stretch to the maximum extent, so that they become as shown in Fig. 251: in this condition the stoma is wide open. When sugar dis-

appears from the guard-cells their suction pressure decreases, and thus water is withdrawn from them to the neighbouring epidermal cells. As a result the guard-cells sag together, and the pore of the stoma is closed (Fig. 251).

The guard-cells alone of the cells of the epidermis contain chloroplasts, and thus they are able to effect photosynthesis. It was formerly assumed that their sugar-content rose as a result of this process. But this is at best only a half-truth. The evidence that photosynthesis is not the direct cause of the opening of the stomata is provided by three simple observations (i) The stomata will open on exposure of the plant to blue light, which has but little stimulating effect on photosynthesis. (ii) The stomata will open in an atmosphere free from carbon dioxide if the plant be exposed to light. In this case photosynthesis could not occur at all. It has, in fact, been demonstrated that carbon dioxide-free air gives a wider opening of the stomata in light and a less complete closure in darkness than does ordinary air. This suggests that, in normal conditions, the concentration of carbon dioxide in the sub-stomatal cavity is an important factor. (iii) The stomata in the white parts of variegated plants will open in spite of the absence of chlorophyll. Again no photosynthesis is possible. But the only perceptible action of light on the contents of the guard-cells is to cause the disappearance of starch and the increase of sugar concentration, which may be tested for. It remains for these two phenomena to be explained. It was suggested by Lloyd in 1908 that light activated an enzyme, which brought about the solution of the starch grains, thus accounting at the same time for the rise in concentration of sugars. Further work by Sayre (1923) and Scarth (1926) has shown that the disappearance of starch occurs only when the hydrogen ion concentration is within certain very narrow limits, beyond which starch is re-formed. They employed dilute solutions of ammonia and acetic acid, and were able to induce starch formation and disappearance and hence stomatal closure and opening. The effect of light would appear, then, to be due to its influence on the hydrogen ion concentration, probably as a result of a photochemical reaction. The following sequence of events, involving the participation of phosphoric acid, has recently been suggested:

$$\text{Starch} + H_3PO_4 \underset{\text{Starch phosphorylase}}{\rightleftharpoons} \text{Glucose monophosphate}$$

$$\text{Glucose monophosphate} + H_2O \underset{\text{Phosphatase}}{\rightleftharpoons} \text{Glucose} + H_3PO_4$$

The forward reaction presumably occurs in the presence of light and the reverse in darkness. It is possible that photosynthesis, or some part of it, may play some part in stomatal opening, since it is accompanied by a disappearance of carbon dioxide and hence of carbonic acid, so that the concentration of hydrogen ions falls. The movements of the stomata

would appear to be affected only very slightly, if at all, by the relative humidity of the atmosphere or the water-content of the leaf. It has also been suggested that hydrogen ion concentration affects the condition of proteins within the guard-cells, causing them to expand or contract, and thus mechanically to regulate the extent of distension of the guard-cells.

Storage of Food

At certain times animals and plants obtain or manufacture more food-material than is required for immediate consumption. Accordingly a portion of it is set aside, and for this purpose definite organs are generally employed.

STORAGE IN ANIMALS. One of the most important of stored foods, at any rate in vertebrates, is the glycogen of the liver, already referred to (page 371). In the portal blood-stream fructose and galactose become converted into glucose, and it is this compound from which glycogen is formed, the formation being stimulated by the high sugar-content of the blood and by insulin (page 485). The reverse process is accelerated by a low concentration of sugar in the blood, low temperature and by adrenalin (page 484). Fats are stored in animals, though no special organ is employed for this purpose. They are deposited principally in layers beneath the skin and around some of the organs within the body-cavity. Such storage is particularly apparent in animals which hibernate, the stores set aside in this way in the summer being consumed during hibernation. The layer of fat formed beneath the skin of the whale and known as the blubber is important in the conservation of the body-temperature of that animal. The hump on the back of a camel is almost entirely fat, and thus enables that animal to exist for a considerable time without food. The camel is also of importance on account of its ability to store water. This is effected by the peculiar nature of the lining of the stomach, which is thrown into copious folds and water preserved in the pouches thus formed. Proteins are not stored in the animal body, nor are mineral salts. The commonest form of storage organ is the egg of many animals, the accumulated yolk serving as a source of nourishment to the developing embryo.

STORAGE IN PLANTS. In plants by far the commonest form of carbohydrate reserve is starch. The so-called *transitory* starch is that which, formed during the day as a means of removal of some of the sugar from circulation, disappears again in darkness with the re-formation of sugar. This starch takes the form of small grains, formed within the chloroplasts. Starch may be stored in a more permanent form, as that accumulated in large storage-organs, such as the potato. This starch takes the form of much larger grains than those of transitory starch, and is formed within the colourless leucoplasts (page 305). The grains may best be examined by scraping the cut surface of a potato, and mounting the

material thus obtained in a drop of water. Each consists of a point of origin, known as the *hilum*, around which the starch is arranged in the form of concentric rings, this arrangement indicating their manner of growth. In some grains the point of origin is asymmetrically placed, so that the grains themselves are described as *eccentric*, whilst in *centric* grains the point of origin is at the centre.

Inulin, like starch, is a complex polysaccharide, but differs from starch in that it is soluble. But on account of its very high molecular weight it exerts a very small osmotic pressure (see text-books of physical chemistry for explanation of this fact), and is therefore a suitable form of carbohydrate for storage. It is especially common in the Compositae and occurs in many Monocotyledons – e.g. the wild hyacinth.

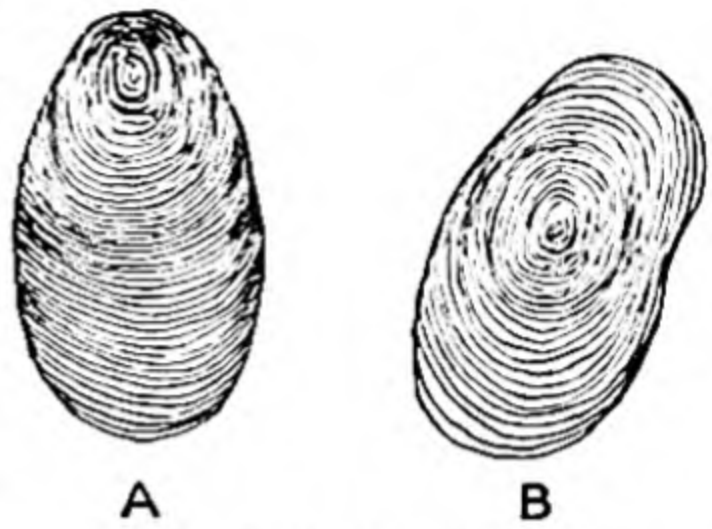


FIG. 252 – Starch grains.
A. Eccentric; *B*., Centric.

Sugars, though formed so universally in green plants, are of little use as storage substances, since they are very soluble and, owing to their relatively low molecular weight, generate high osmotic pressures. They do, however, make occasional appearances as reserve food. Glucose, for example, occurs in the bulb of the onion, whilst sucrose is found in the sugar beet and in the stem of the sugar cane. The sugars (fructose) found in succulent fruits and in nectar are not storage products, for the former assists in seed-dispersal, encouraging animals to eat the fruits, whilst the latter is important in the process of pollination. The maltose found in many starch-containing seeds is formed as a result of the hydrolysis of the starch, and is not itself the primary form of stored carbohydrate. Glucose may occur in the form of a complex substance, known as a glucoside. This is not a simple carbohydrate, but is combined with aromatic and other organic substances. An example of such a body is the *amygdalin* of the bitter almond. An enzyme, *emulsin*, present in the skin of the seed brings about the liberation of the glucose.

Unlike animals, plants carry considerable protein reserves. Storage-organs frequently contain proteins in the form of crystalline bodies, known as *crystalloids*, found usually associated with the plastids: such occur, for example, in the outer layers of the potato. Other proteins are carried in solution. Proteins may also take on the form of comparatively large grains, known as *aleurone* grains. These are particularly common in oil-containing seeds – e.g. castor oil. Before such reserve food can be rendered available to the plant it must be converted into diffusible form, this being accomplished by appropriate enzymes. The commonest product of enzyme-action on proteins is, as in animals, an amino-acid.

Fats and oils constitute an important group of food-reserves. They are

commonest in seeds, though oil-globules do appear in vegetative cells. The castor oil seed is an important example of an oil-containing storage-organ. As in animals the fats and oils are decomposed into their constituents – glycerol and a fatty acid – by enzyme action prior to distribution. In general, oils and fats, though formed from carbohydrates, are found principally in seeds where the supply of the latter class of compounds in the endosperm is negligible or entirely absent.

Types of Nutrition

Animals and plants may be classified according to their mode of nutrition. Thus the typical mode of animal nutrition involving the taking in of solid, complex, organic food and its subsequent digestion, absorption and distribution (if this be necessary), is described as *holozoic*. Nutrition involving photosynthesis, characteristic of all green plants, is described a *holophytic*. The vast majority of animals are holozoic in their mode of nutrition, and of plants holophytic. There are two further types of nutrition, however, one of which occurs exceptionally in both the animal and plant kingdoms. *Saprophytic* nutrition involves the taking in of liquid, organic food and its subsequent treatment in a manner analogous to that of ordinary digestion. This type of nutrition is confined to certain plants not possessing chlorophyll. *Mucor* and *Agaricus* (mushroom) afford instructive examples. *Mucor* lives on the majority of decaying substances, amongst which may be mentioned bread and manure. The hyphae (page 203) penetrate the substratum on which the plant is growing, and enzymes produced by their walls render the essential food-compounds soluble and assimilable. Thus the food does not enter the body of the plant until it is liquid in form. *Agaricus*, growing in soil in which there is an abundance of organic material, behaves similarly. After absorption the materials are built up into the protoplasm of the plant. A few animals may be said to be *saprozoic* in their mode of nutrition (see below). Certain animals and plants are designated as *parasites*. The criterion of a parasite is that it obtains its nourishment from another living organism, animal or plant. This means that it does not have to subject the food taken in to the chemical processes usual in an animal or plant. Thus an animal parasite may obtain its food ready digested. *Taenia* affords an example of such an organism. Living in the intestine of various mammals, according to species, it absorbs its food through the general body-surface, thereby eliminating the problem of distribution as well as of digestion. Many animal parasites, however, have to effect digestion of their food, though they do obtain it already in solution. This mode of nutrition corresponds to the saprophytic type exhibited by some plants, and is thus termed saprozoic. *Plasmodium* is a parasite, living within the red blood corpuscles of man. The organism from which a parasite obtains its subsistence is termed its host. Examples of plant parasites are numerous. They are well represented amongst the

Fungi, but are not confined to that group. Thus *Pythium* and the potato blight are examples of plant parasites from the Fungi, whilst all the pathogenic Bacteria are necessarily parasitic. It will be apparent, therefore, that almost all members of the Fungi and Bacteria are parasitic or saprophytic, as indeed must be the case, owing to the absence of chlorophyll.

Finally, there must be mentioned a small group of Bacteria whose nutrition does not properly belong to any of the four classes mentioned above, though it has certain affinities with the holophytic type. They build up their protoplasm by a process known as **chemosynthesis**. Starting from carbon dioxide and water these compounds are built up into sugars, but the energy required for this process is not provided by light. Oxidation of certain substances in the surrounding medium is effected by the Bacteria, and this process liberates the energy necessary for the chemosynthesis of sugars. Thus hydrogen sulphide is oxidised by *Beggiatoa* to sulphur and water, whilst *Nitrosomonas* and *Nitrobacter* effect respectively the oxidation of ammonia to nitrites and of nitrites to nitrates: for this reason they are of primary importance in the soil.

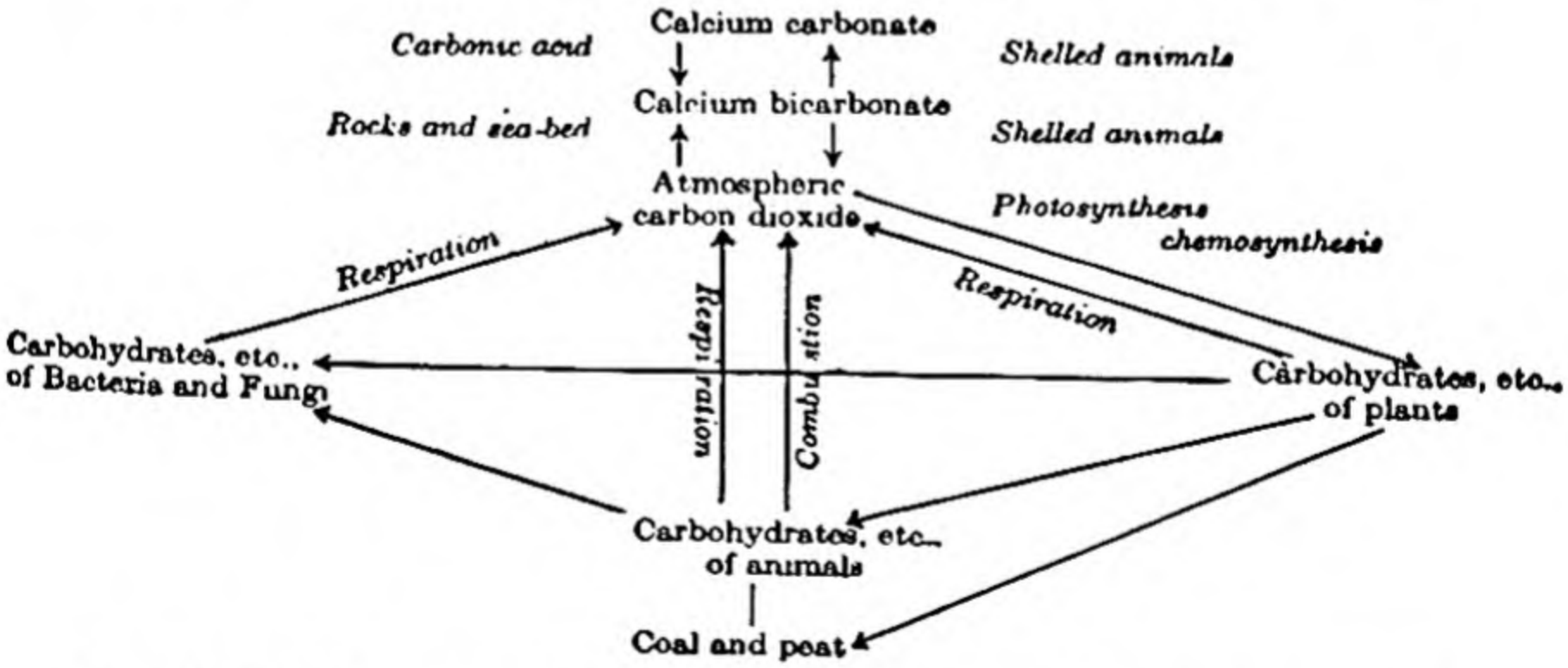
$$(NH_4)_2CO_3 + 3O_2 = 2HNO_2 + CO_2 + 3H_2O + 148 \text{ calories.}$$

The nitrous acid so formed is neutralised by calcium carbonate with the formation of calcium nitrite, which is then oxidised.

$$2NO'_2 + O_2 = 2NO'_3 + 22 \text{ calories}$$

Nutritional Relationship Between Animals and Plants

In conclusion it is necessary to consider how animals and plants contrive to prevent an eventual cessation of their supply of food, which might



at first sight be expected to result from the continuity of the demand. It is evident that all living organisms must obtain their energy eventually from the sun, and a study of simple food-chains, as they are called, will show that this must necessarily be effected through the intermediary of

plants. Thus, if animal *A* preys principally on animal *B*, and this in its turn on animal *C*, and so on, eventually the chain will end with an animal whose food is provided by plants. To take a simple example, large birds, such as the hawk, may feed on smaller birds, which in turn feed on earthworms and grubs. These obtain their nourishment either from fresh vegetable-matter, as do the various aphids so harmful to many crops, or from the decayed vegetation in the soil, as do earthworms. Thus, in general, animals depend directly or indirectly on plants. But even allowing for this there must obviously be a circulation of essential food-substances, and in this respect the relationship between animals and plants is a very important one. Holophytic nutrition in green plants results in the removal of carbon dioxide from the atmosphere and its replacement by oxygen. Such plants, and the animals which obtain their nourishment from them, respire, and this, as shown in more detail in Chapter 24, results in the oxidation of sugars, accompanied by the evolution of carbon dioxide. This is returned to the atmosphere. Plants are not always destroyed by animals, and a great many have survived and undergone subjection to great pressures, resulting in the formation of peat and coal. These, in turn, are burned by man, carbon dioxide being again liberated. The putrefaction of the bodies of dead animals and plants also results in the liberation of carbon dioxide, all such processes being effected by Bacteria. The diagram on page 409 will serve as a summary of the facts concerning the circulation of carbon.

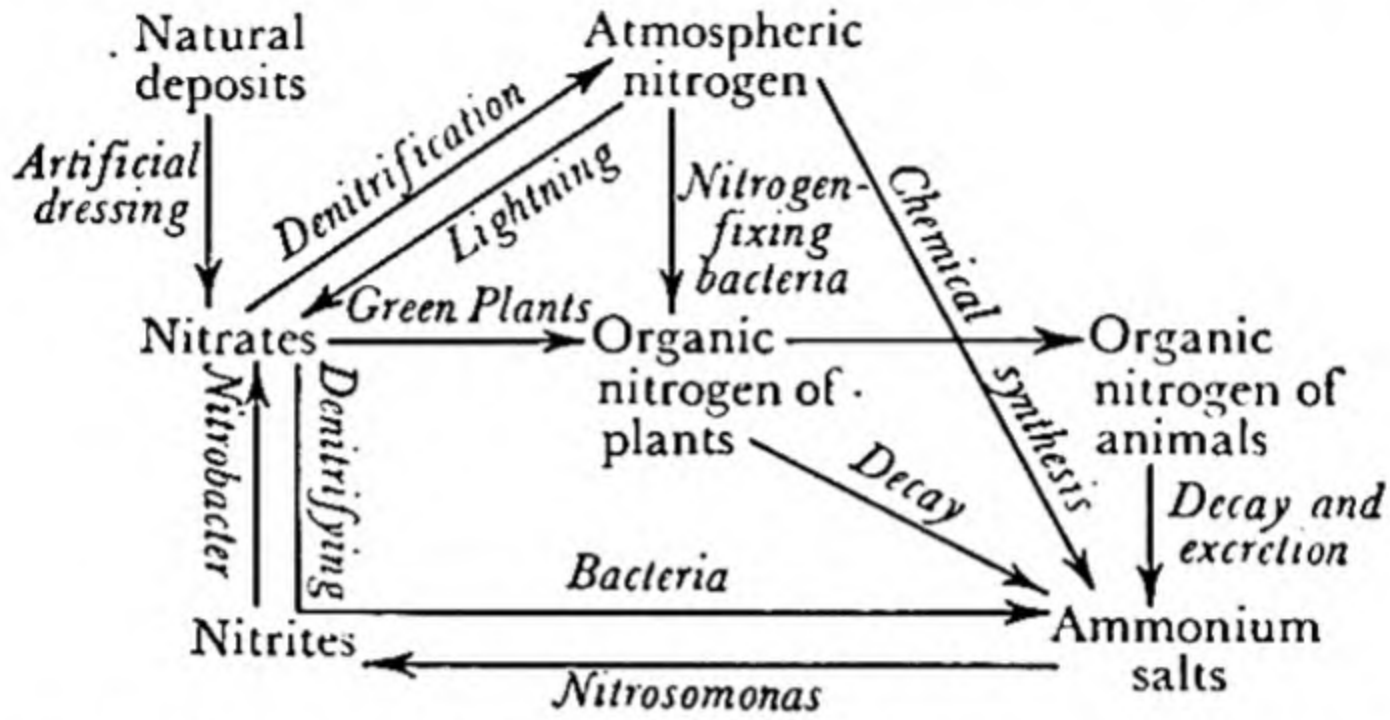
THE NITROGEN CYCLE. It will be recalled that nitrogen is an invariable constituent of proteins, and therefore the circulation of this element is equally important with that of carbon. Animal proteins are derived from those of plants through food-chains, and these two classes of substances may be termed, for present purposes, organic nitrogen. Its subsequent decomposition may result from one of a number of events. The body of the animal or plant may die, its tissues and their contents then undergoing putrefaction. The animal may discharge nitrogenous waste matter, or the leaves of a tree may be shed. In any case the nitrogen-content of the substances thus liberated is converted by Bacteria into an ammonium salt, usually the carbonate, owing to the presence of carbon dioxide and water. Thus urea, an extremely common nitrogenous constituent of animal waste, is hydrolysed at the instance of Bacteria.

$$CO(NH_2)_2 + 2H_2O \rightarrow (NH_4)_2CO_3$$

As already mentioned on page 409, the ammonium salt thus formed is oxidised by a soil Bacterium, *Nitrosomonas*, into a nitrite, and this is further oxidised by a second Bacterium, *Nitrobacter*, with the formation of a nitrate. Nitrates thus formed are absorbed by green plants, and their nitrogen is eventually converted into organic form. Whilst this is the main part of the circulation of nitrogen there are subsidiary reactions to be taken into account. One of these is represented by the peculiar ability

of some plants to 'fix' atmospheric nitrogen – i.e., to use it as their ultimate source of combined organic nitrogen.

Whilst many species of blue-green Algae are possessed of this power, it is principally amongst Bacteria that the process of fixation occurs. Thus there occur freely in the soil species of two distinct genera – *Clostridium pasteureanum* and *Azotobacter chroöcoccum* and *agilis*. The first named is an obligate anaerobe, whilst the *Azotobacter* species are aerobic.



Fixation is also practised by all photosynthetic Bacteria – e.g., *Chromatium* and *Chlorobium* (see page 413), as well as by *Desulphovibrio* (page 414). Perhaps the best-known example of fixation is provided by *Rhizobium* (formerly known as *Bacillus radicicola*), which lives in symbiotic association with members of the family Leguminosae, where it is responsible for the formation of the characteristic root-nodules. It would appear that actual symbiosis is an essential condition for the fixation process, since there is something more involved than a mere supply of carbohydrate material by the flowering plant. Thus haemoglobin is formed in healthy nodules, imparting a pinkish colour, but not by either partner alone. It has been estimated that the stems and leaves of a clover crop receive the equivalent of 14 cwt. of ammonium sulphate per acre as a result of the activities of *Rhizobium*. A similar association has been described in the alder, as well as in some sub-tropical genera. In some lichens (page 671) the algal partner is believed to be nitrogen-fixing, though recent work has shown that most lichens contain *Azotobacter*, thus furnishing an example of a triple alliance. It may, in fact, be the Bacteria which fix the nitrogen.

Some plants capable of independent fixation associate symbiotically with others impotent in this respect. This is true of some blue-green Algae, found occasionally as symbionts with liverworts, ferns and even Spermaphyta.

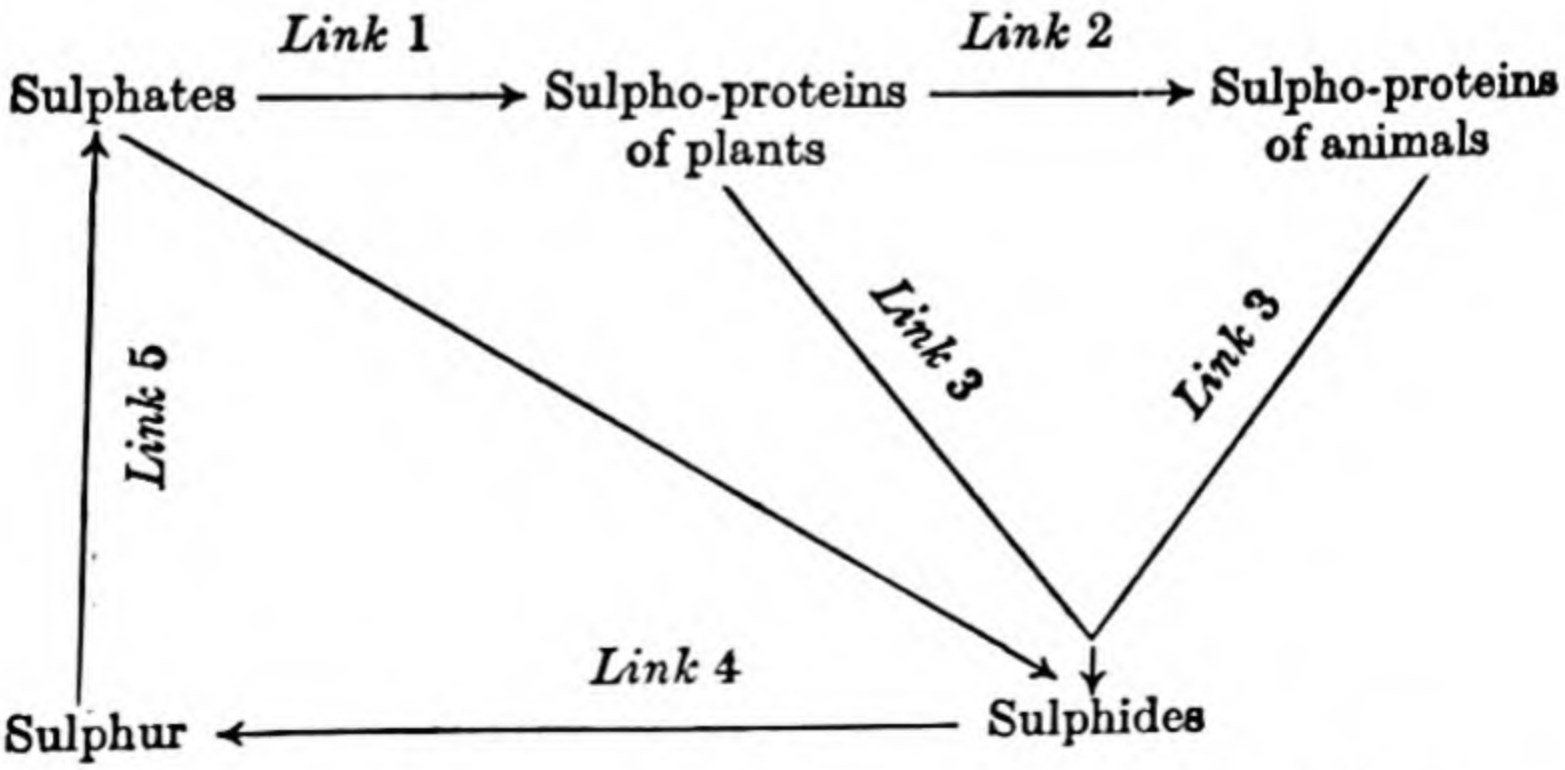
The mechanism by which fixation is brought about has been the object of much research. It occurs only in living tissues and is essentially an

endothermic reaction, accelerated by an enzyme-complex collectively termed *azotase*. The probable sequence of compounds along the fixation path has been investigated by the use of nitrogen containing a higher proportion than usual of the 'heavy' isotope (N = 15), followed by analysis with a mass-spectrometer after a short interval. This has revealed that the greatest proportions of the 'heavy' nitrogen occur in glutamic acid. As already indicated (page 401) this is believed to be the compound via which ammonia makes its entry into the nitrogen metabolism of the normal plant. Thus it appears that, in the fixation process, ammonia or some closely-allied substance, such as hydroxylamine (NH_2OH), is the key intermediate compound. Further proof of this is suggested by the fact that increased ammonia supply frequently depresses the rate of nitrogen fixation.

For further reading on this subject the student is recommended to 'Nitrogen Fixation', by G. E. Fogg, in *New Biology*, No. 18 (Penguin Books), to which article the author is greatly indebted for much up-to-date information.

Under certain circumstances, notably a shortage of free oxygen and an abundance of readily-oxidised organic material, some soil Bacteria bring about a reversal of the normal process of nitrate-formation, nitrates being reduced first to nitrites and eventually to ammonia. This is known as denitrification, since it reduces the amount of nitrogen in a form available to green plants. The table on page 411 serves to summarise the various phases in the distribution of nitrogen.

THE SULPHUR CYCLE. As with nitrogen, Bacteria play an important part in the circulation of the element sulphur, which is a constituent of many proteins of both animals and plants. The principal



features may first be summarised by means of the diagram above.

Link 1. Sulphates represent the form in which sulphur is available to green plants. Having been absorbed the sulphates are presumably first

subjected to a reductive process akin to that for nitrates (page 400), after which the resulting compounds are assimilated into organic form.

Link 2. Animals require their sulphur in organic form and therefore must derive it from plants either directly, as in the case of herbivores, or indirectly through the operation of food chains.

Link 3. Just as the contained nitrogen of the proteins of living organisms is ultimately liberated in the form of ammonia, so the sulphur of sulpho-proteins is converted into sulphides, including much hydrogen sulphide, by the putrefaction of waste matter and eventually of the dead bodies of the organisms. This putrefactive process is accomplished by a wide diversity of Bacteria and Fungi, including both aerobic and anaerobic forms. Many of them inhabit the soil.

Link 4. The oxidation of sulphides to sulphur is performed by two distinct groups of Bacteria, one colourless and the other coloured. The former basically perform the type of reaction exemplified by the following equation –

$$2Na_2S + O_2 + 2H_2O \rightarrow 2S + 4NaOH + \textit{energy}$$

The caustic soda is neutralised by the carbon dioxide invariably present, producing a mixture of carbonate and bicarbonate. *Beggiatoa* (page 397) is an example of this group. Granules of sulphur are deposited within its cells, and these can be utilised by oxidation to sulphuric acid if the supply of sulphide fails.

Of the coloured forms, *Chromatium* (red) and *Chlorobium* (green) have been investigated. Both are anaerobes and both require light, since they perform what is essentially a photosynthetic process, but employ hydrogen sulphide (H_2S) instead of water (H_2O) as the source of hydrogen for carbohydrate formation.

Green Plants $\quad CO_2 + 2H_2O + \textit{energy} \rightarrow (CH_2O) + H_2O + O_2$

S Bacteria $\quad CO_2 + 2H_2S + \textit{energy} \rightarrow (CH_2O) + H_2O + 2S$

These Bacteria have been observed to form well-defined layers deep in the waters of some American lakes, where they prevent pollution by converting the sulphides resulting from putrefaction on the bed of the lakes into harmless sulphur. With further investigation this may provide a method of combating much pollution of inland waters.

Link 5. The oxidation of sulphur to sulphates is effected by a small and specialised group of Bacteria, believed by some authorities to constitute a single species. A widely studied example is provided by *Thiobacillus thio-oxidans*. This organism is an obligate aerobe and depends also upon the presence of water for its activities, although the thin film adhering to particles of soil or other bodies is adequate. It is responsible for the type of reaction represented by the equation –

$$2S + 3O_2 + 2H_2O \rightarrow 2H_2SO_4 + \textit{energy}$$

The energy liberated is used in chemosynthesis for the building up of carbohydrates from carbon dioxide and water. These Bacteria are, in

fact, autotrophic, being unable to make any use of organic matter. They are very tolerant of the sulphuric acid they create and can survive in solutions of strength greater than Normal. Apart from their service in rendering sulphur in a form suitable for absorption by green plants, they are economically important on account of the corrosion of buildings which they cause in industrial areas, where the atmosphere is polluted with sulphur and its simple compounds with hydrogen and oxygen.

The closely related *Thiobacillus denitrificans* is able to use nitrates as its source of oxygen to perform the same reaction and is therefore capable of life in the absence of free oxygen.

Sulphates to Sulphides. It will be noted from the diagram of the sulphur cycle that some sulphate material is wasted by conversion into sulphide. Although the reactions involved are apparently of no value in maintaining the continuity of sulphur supplies to living organisms, they are of considerable economic importance and so will be briefly considered here. The Bacteria responsible are all anaerobes, using sulphates as oxidising agents, sulphides being by-products. The species mainly concerned is *Desulphovibrio desulphuricans*. It can tolerate a high salt concentration, high pressure and very high temperatures (up to 80° C). By reducing natural sulphates in seas and inland waters to sulphides, which are poisonous to animal life, they cause considerable pollution. Further, since they are able to use free hydrogen (on the few occasions when this element is available) in the reduction of sulphates, they are responsible for much corrosion of iron pipes. Such corrosion is due initially to the reaction –

$$Fe + 2H_2O \rightarrow Fe(OH)_2 + H_2$$

This hydrogen normally accumulates to form a protective covering if the water in or around the pipes is reasonably air-free, but in the presence of these sulphate-reducing Bacteria this hydrogen is utilised in the reductive process, since natural waters always contain a supply of sulphates.

On the credit side, however, these same Bacteria are largely responsible for most of the world's sulphur deposits. It is believed that the Texas deposits, yielding over 90% of the world's sulphur, were formed by the reduction of the calcium sulphate of the sea water, when part of the Gulf of Mexico dried up, into sulphides, which were subsequently oxidised to sulphur, either spontaneously or by Bacteria of the type discussed in Link 4.

The student who wishes to learn more of the activities of sulphur Bacteria is referred to the article by John Postgate in *New Biology*, No. 17 (Penguin Books).

PRACTICAL WORK

Digestion of Starch

Make into a pulp with a small quantity of water a little raw potato.

Place this in a test-tube. Allow some saliva to flow from the mouth into the test-tube and leave the mixture to stand for half an hour. Add a little more water to the mixture, warm and filter. Any sugars now formed will be present in the filtrate. Test for them as detailed on page 384. Discover in this way whether a reducing sugar or otherwise is formed by the digestion of starch, according to whether or not the monosaccharide tests work before boiling with a few drops of concentrated hydrochloric acid and subsequent neutralisation.

Villi

Examine a transverse section of the intestine of the frog. Notice that the lining is thrown into folds, each of which is a villus. See Fig. 248, page 393.

Extraction of Chlorophyll

Chop up some leaves and put into a flask with some 80% acetone. The chlorophyll dissolves in the acetone, which becomes green in colour. Allow some of it to stand, when minute crystals appear as the result of evaporation. Place a drop of the solution on to a clean filter paper. Soon this appears as a green disc surrounded by a yellow circle. This is because the yellow pigments travel more rapidly than the green.

To show the evolution of Oxygen by Plants

Set up the apparatus shown in Fig. 253, using a foliaceous water-weed as the necessary plant material. Expose to fairly bright sunlight, when bubbles of gas will be found to collect in the test-tube. This gas may be shown to contain a greater proportion of oxygen than does atmospheric air.

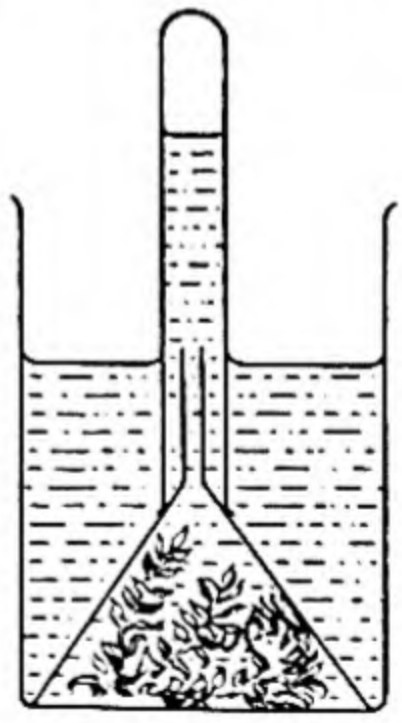


FIG. 253 – Apparatus for the demonstration of the evolution of oxygen by a water-weed in sunlight.

The presence of Starch in a Green Leaf

Strip off a leaf from a plant which has been exposed to sunlight for a long period. Immerse the leaf for a short time – fifteen seconds – in boiling water, thus killing the leaf. Place it in some 80% acetone until it is almost white, the chlorophyll having been dissolved out. Immerse it in a solution of iodine in benzene, when the leaf becomes dark blue in colour owing to the presence of starch.

Repeat the above experiment with a leaf taken from a plant previously kept in darkness for not less than twenty-four hours. No coloration is produced with iodine, indicating the absence of starch.

The necessity of Carbon Dioxide

Choose two similar plants in pots and after retention in darkness for twenty-four hours set them up in the apparatus shown in Fig. 254. In one case the air entering the bell-jar is forced to do so through a U-tube packed with soda-lime, which absorbs carbon dioxide, whilst in the other

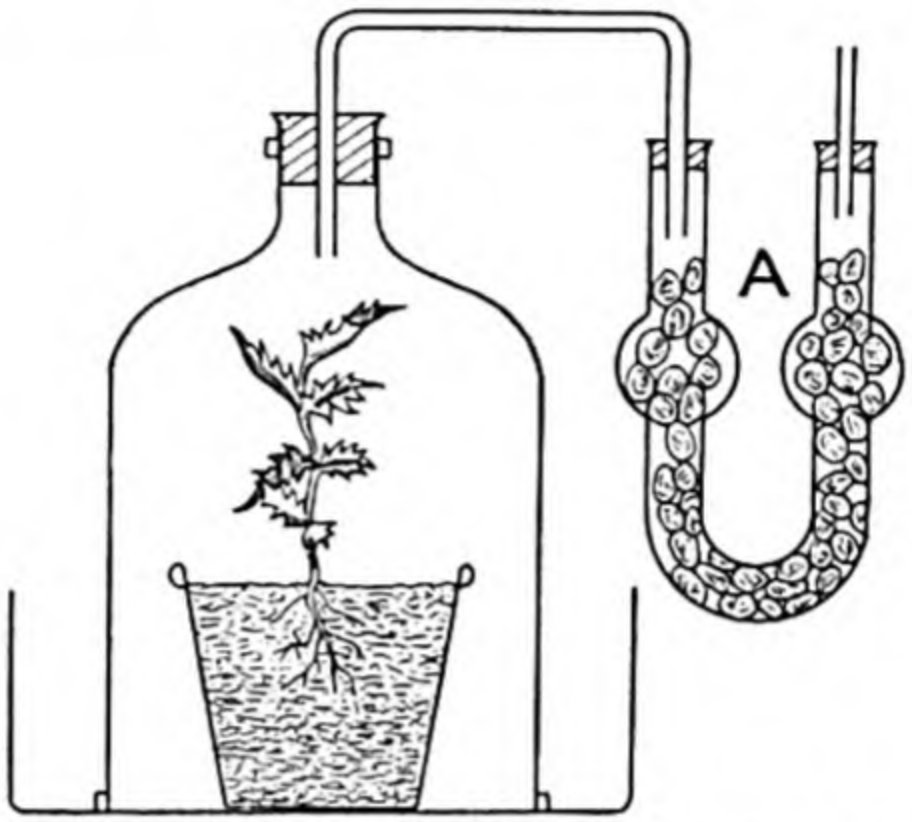


FIG. 254 – Apparatus for the demonstration of the necessity of carbon dioxide to a green plant.

case no soda-lime is employed. Place both plants in sunlight for several hours, and then test a leaf from each for the presence of starch. It is found that the plant deprived of carbon dioxide fails to form starch.

Presence of Glucose in the Onion

Boil an onion, chopped into pieces, with a small quantity of water. Filter. Test the filtrate for glucose (page 384).

Root Nodules

Examine roots of mature bean plants (*Vicia faba*), whole and in transverse section, noting the distribution and structure of the root nodules.

CHAPTER 24

Growth and Respiration

GROWTH

Food taken into the body normally fulfils one of two purposes. Either it is completely assimilated, resulting in the formation of new protoplasm, or else it provides the fuel, through the oxidation of which energy is rendered available to the animal or plant. New body-substance is required to make good the general wear and tear of the tissues, but, dependent upon the rates at which these two essentially opposed processes of assimilation and destruction occur, it is possible that the net quantity of protoplasm may be increased. Growth has thus been aptly defined as the final expression of successful metabolism. For it to occur anabolism and katabolism must take place. Anabolism results in the production of new body substance, whilst katabolic processes provide the requisite energy for growth. Fundamentally growth is identical in animals and plants, but the latter present certain peculiar responses to environmental conditions, and have thus been the object of more extensive experimentation. The following consideration of the phenomenon of growth will therefore concern itself chiefly with plants, though reference to parallel characteristics in animals will be made as the occasion arises.

Space-analysis of Growth

Growth in flowering plants is peculiarly localised at the tips, in sharp contrast to the roughly uniform rates of growth of all parts of an animal body. In the plant three main regions may be observed for both root and shoot. At the extremity is the *primary meristematic region*, composed of compact cells undergoing continuous division and where combustion and assimilation are rapid. Behind this comes the *region of primary enlargement*. Here the cells absorb water by imbibition and osmosis, as well as through the increase in the extensibility of their walls, brought about by auxins (see page 492). Much carbohydrate is required for the formation of cell-walls, while outer dermal tissues become stretched as inner cells elongate. Finally come the *maturing primary regions*, where cells assume their final, and often specialised, forms. These are determined by a combination of inherited characters and environment. Specific substances are elaborated in precise conditions – e.g. iron and blue-violet light are required for the formation of chlorophyll. Temperature is important. For example, the flowers of *Primula sinensis*, var. *rubra*,

are normally red, but if the plant is grown in a hothouse they are white: the normal spines of broom become short leafy shoots if this plant is grown in a very moist atmosphere.

Measurement of Growth

Growth may be measured in a variety of ways, but of these only one yields results which cannot easily be misinterpreted. The really significant feature of growth is that it results in the formation of new protoplasm. This should obviously be capable of estimation through measurements of increase in dry weight. The mere absorption of water does not necessarily indicate that growth has occurred. Thus, for example, during germination the wet weight increases, whilst the dry weight actually shows a decline. Barley is suitable material for the estimation of growth by determination of dry weight at fixed intervals. Thus, perhaps a hundred barley plants may be grown in conditions maintained as nearly as possible uniform, and at periods of a week ten may be selected at random and their dry weight determined. This is done by placing them in a dish and heating the whole over a water-bath until the weight remains constant. At the same time other measurements, including net weight, length and number of leaves, may be made.

The apparatus employed for measurement of increase in length will now be described, but it must again be emphasised that the results so obtained are not a reliable index of true growth. Thus a plant grown in darkness will increase more rapidly in length than one subjected to light Yet the latter alone can produce new protoplasm, since it alone is capable of effecting photosynthesis. Measurement of mere increase in length would further suggest, for example, that *Convolvulus* grows more quickly

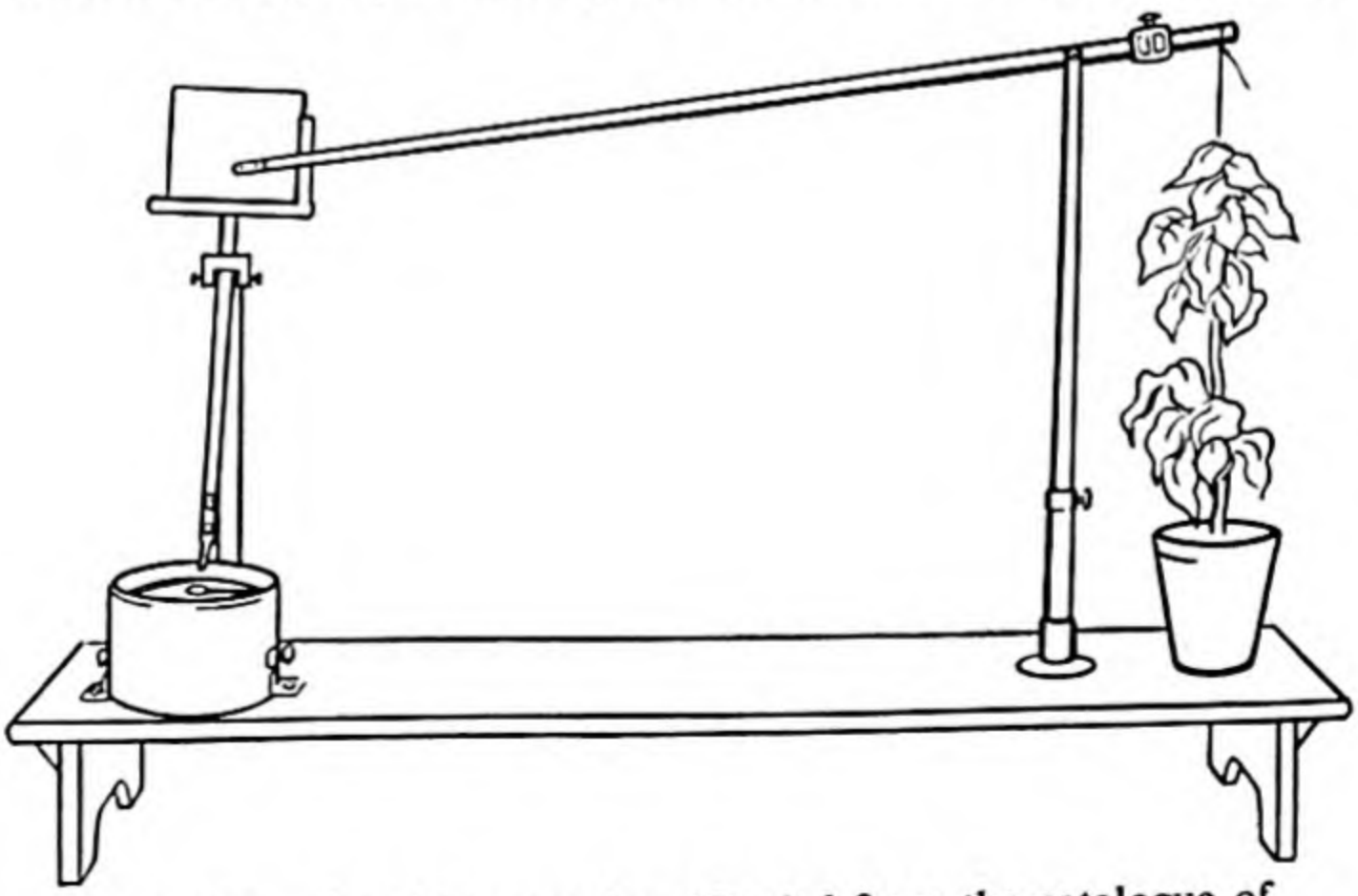


FIG. 255 – An Auxanometer. (Copied from the catalogue of Messrs. Flatters & Garnett, Ltd.)

than does wheat. But this does not take into account the fact that the wheat plant gives off branches at its base, whereas *Convolvulus* does not. Increase in length of a plant, or of a single part of it, is measured by means of an **auxanomter**. This consists of a delicately-adjusted lever, one end of which is attached by thread to the plant whose length-increase is to be determined. The other end is in contact by means of a fine pointer with a smoked-glass screen. At intervals of an hour the screen is moved across the pointer by means of the minute-hand of a clock, placed at the base of the pivoted support of the screen. As growth occurs the end of the lever attached to the plant is raised, whilst the other is accordingly lowered. Since the latter arm of the lever is considerably the longer the 'growth' is considerably magnified prior to its being recorded. Thus the increase in length is marked by a series of parallel scratches on the smoked screen (Fig. 255). The instrument is useful in that it can be made to measure 'growth' not only of different parts of a plant, but also to determine the effects of external conditions on the rate of 'growth'.

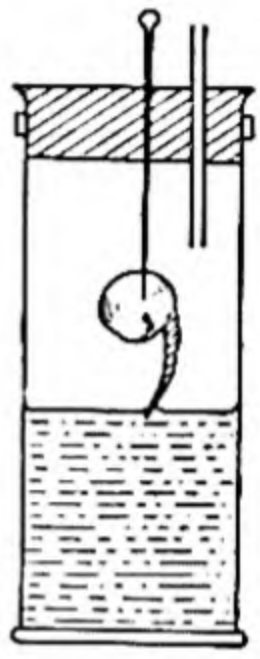


FIG. 256 – Apparatus for the demonstration of the region of maximum elongation of the radicle.

A further method of measurement of the elongation of the radicle and plumule of a seedling also serves to show at what regions in the plant such elongation is at a maximum. A germinating bean seedling is fixed to the end of a long pin passing through a cork into a vessel containing water, the tip of the root being just in contact with the water. At the outset of the experiment small ink marks are made on the radicle at equal distances apart. As the radicle elongates it can be drawn up on the pin so that the tip at any time just reaches the surface of the water. If the radicle be later examined it will be found that the marks

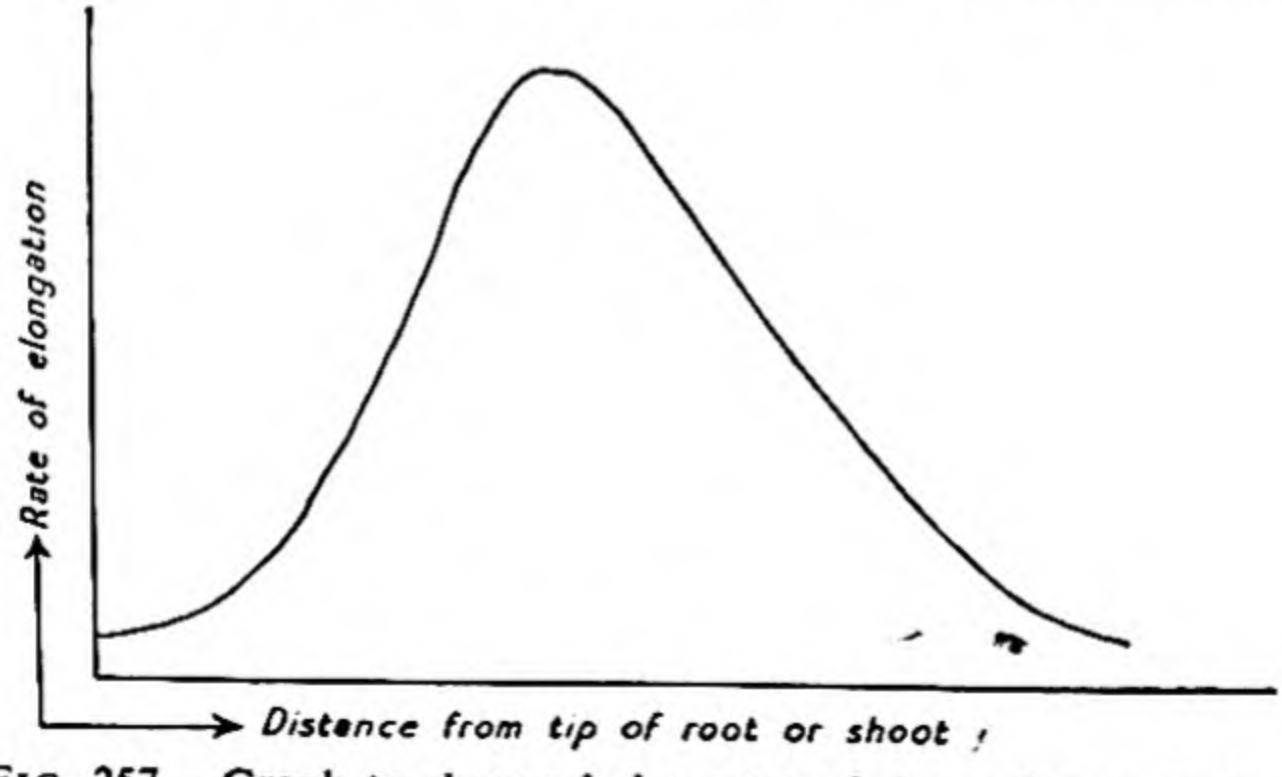


FIG. 257 – Graph to show relative rates of elongation at various distances from the root-tip.

near the tip will now be slightly further apart, whilst the distances between the marks just behind this region will have become considerably increased. The marks still further from the tip will show a progressive decrease in their distance of separation, until finally it becomes apparent that no elongation has occurred at all. These results may be made more forcible if they are represented graphically, as shown in Fig. 257. It is apparent from this that the cells near the tip have elongated but slightly, but this elongation reaches a maximum in the somewhat older cells behind them, only to decrease again as the base is approached. These three phases of elongation together constitute the **grand period of growth**. It may be similarly demonstrated for a plumule by means of the apparatus shown on page 418.

Conditions regulating Growth

It is only to be expected that environmental conditions, as well as hereditary propensities, will exert a considerable influence on the rate, and often on the direction, of growth. The former alone will be considered here, since reference is made to directional factors in Chapters 26 and 27.

(A) TEMPERATURE. It has been shown that the rate of growth of pea seedlings increases uniformly up to about 29° C., above which temperature certain irregularities begin to appear. These have been attributed to the differential solubility of various food-substances, the stability of enzymes and the accumulation of waste-products at higher temperatures. The rate of the vast majority of laboratory reactions is known to be approximately doubled by a rise of temperature of 10° C. It has further been established that for growth, maximum, minimum and optimum temperatures exist. At the minimum temperature chemical processes involved in metabolism are necessarily proceeding at their slowest measurable speed, whilst at the maximum temperature growth tends to occur at such a speed that new material cannot be synthesised sufficiently rapidly. The optimum temperature is obviously the one at which the most satisfactory balance is maintained between the anabolic and katabolic phases of metabolism. It is very largely the temperature factor which regulates the geographical distrubution of plants, though often this is on account of its influence upon seed and fruit formation rather than upon vegetative growth.

(B) LIGHT. The most obvious effect of light in the regulation of growth is due to the control it exerts on the process of photosynthesis. Thus, as a result of prolonged exposure to darkness a plant must succumb to carbohydrate starvation. But, quite apart from this, light exerts a considerable influence over the texture and elongation of many parts of a plant. In general, the retention of a plant in darkness results in abnormal elongation of the internodes, the suppression of the leaf laminae, and the formation of soft and weak stems. These deformities are summarised

under the name **etiolation**. They may best be observed by growing in darkness plants which carry plentiful supplies of reserve food, so that they are comparatively independent of the progress of photosynthesis: the potato affords an obvious choice. But it must be remembered that during such periods of excessive elongation the dry weight of the plant actually decreases, so that growth cannot be said to have occurred. Certain plants whose leaves arise from underground stems show abnormal elongation of the petioles if grown in darkness. This fact is made use of in the 'forcing' of rhubarb by the exclusion of light.

Not only is the complete presence or absence of light an important factor in the regulation of growth, but subjection to light for definite periods exerts a marked effect. This can be seen by a careful study of the chart obtained by the use of the auxanometer. The growth marks on the screen will be found to be closest together after noon, showing that elongation is at a minimum, whilst after midnight it rises to its maximum. The intervening periods show progressive declines or increases in rate. Thus a daily period of growth may be referred to. In addition, the phenomenon of **photoperiodism** must be noted. This refers to the influence of day-length – or, more correctly, to the duration of the period of darkness – upon the initiation of flowering. Thus flowering plants may be roughly divided into 'short day' and 'long day' categories. 'Short day' plants require a photoperiod of less than a critical value for successful flowering. Under long day conditions they do not flower, but produce luxuriant vegetative growth. The opposite is the case with 'long day' species. That it is the dark period which is the important factor has been shown experimentally with 'short day' plants, in which one flash of light during the dark period is sufficient to inhibit flowering. It has also been established that the development of flowers, and even of vegetative buds, is, in some cases, dependent upon intensity of light, as distinct from its duration. Thus it is usual to find that marginal buds on a tree mature more readily than those situated within the crown, whilst it is not unusual to observe a greater development of the crown on the south side than on the north. It should be noted that many plants are insensitive to photoperiod.

Experiments have also been carried out in which plants have been subjected to lights of different wave-lengths by being placed under screens which permit the passage of some colours and absorb others. Care has to be taken that all the screens transmit equal quantities of light-energy, or it is not possible to place a correct interpretation on the results. In general it is found that plants deprived of blue-violet light show marked signs of etiolation, thus indicating that light from this end of the spectrum is essential for healthy growth.

(C) ELECTRICITY. Plants subjected to a carefully regulated discharge show considerable improvement upon the normal condition both in weight and colour. The reason for this is obscure, especially as it appears

that the discharge does not materially affect the respiratory or photosynthetic rate.

(D) OTHER CONDITIONS. That an adequate supply of food must be available for true growth to occur is evident. Thus water, mineral salts and carbon dioxide are essential. The *p*H value of the solutions must be within relatively narrow limits, whilst the salt-content must be physiologically balanced. Further, since growth requires energy, oxygen must be present to facilitate the process of respiration. Though plants can breathe anaerobically for some time – e.g., germinating peas – the oxidation of food materials is incomplete, and the accumulation of deleterious end-products will eventually prove fatal.

(E) INTERNAL CONDITIONS. Several conditions contribute to what might be regarded as the internal environment, and their effects on the process of growth will be considered separately.

(*a*) *Meristematic tissue* must be present and in an active state. In some families of flowering plants – e.g. the Rosaeae – it has been demonstrated that there is an essential period of dormancy between the ripening of seeds and their subsequent germination.

(*b*) *Food reserves* must be present, rendered available as required. This condition applies, of course, only to seedlings or plants in process of development from vegetative organs of propagation.

(*c*) There must be a *state of turgor*, generated by the entry of water. This has much to do with the elongation of cells in the near-apex of root and shoot.

(*d*) *Growth hormones* must be produced. These substances are discussed on page 488. It is possibly the time taken for them to be elaborated in active form in some plants which affords an explanation of essential dormancy (see [*a*] above).

Circumnutation

There is one aspect of the direction of elongation which may well be considered here. As already stated, elongation of the shoots occurs at the apex, though it is found on close observation that the path traced by the growing point is not a straight one. This pursuit of a somewhat irregular path by the tip of the shoot is known as **circumnutation**. Before it can be satisfactorily demonstrated it must needs be considerably magnified, for the departure from a straight course is but slight. The apparatus shown in Fig. 258 may be employed. It consists of a frame with a plate of glass in the roof. The runner bean affords suitable material for experimentation, and a young seedling growing in a pot is placed within the frame. From one of the supports projects a pointer, fixed in such a position that its tip, when viewed from above, is in a straight line with the length of the stem. At intervals small strips of gummed paper are pasted on the glass roof in such a way that their apices are in alignment with the tip of the pointer and the growing tip of the stem. The general tendency is

to the pursuit of a spiral course, so that the strips of paper come to lie with their apices approximately on the circumference of a circle. This phenomenon may be accounted for by the assumption that the rate of elongation is greater on one side of the apex, and that the zone of maximum elongation is continually shifting its position.

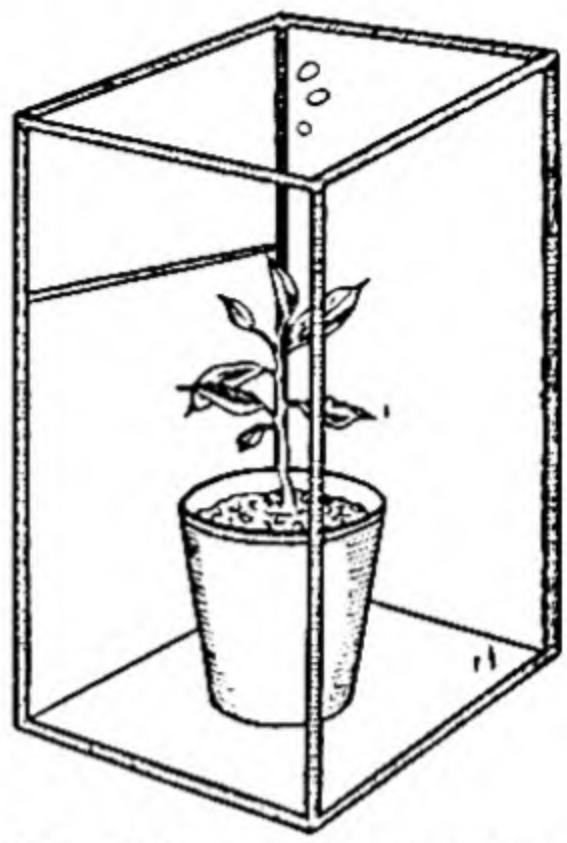


FIG. 258 – Apparatus for the demonstration of circumnutation.

Growth in Animals

Apart from food supply it would appear that animal growth is much less dependent on external conditions than is that of plants. Growth is much more uniform in animals, taking place at approximately equal rates throughout every part of the organism, though there are exceptions to this – e.g. human hair. Thus there is but little change in shape between the young and adult organism, growth resulting only in an increase in size. In both animals and plants growth takes place by the incorporation of new material throughout the bulk of the tissues, in sharp contrast to the growth of inanimate matter – e.g., a crystal of copper sulphate suspended in a saturated solution of that salt – where growth occurs as a result of surface accretion.

RESPIRATION

Respiration

The living organism is continually requiring available energy, and this it must obtain from the substances which provide its food. Complex chemical substances contain large reserves of potential energy, and it is the chief function of respiration to convert this into kinetic form. This is fundamentally true of both animals and plants, and, whilst the mechanism accommodating respiration is different in the two groups, the process remains essentially the same. Animals require a great deal more energy than do plants, for their characteristic motility alone necessitates a considerable expenditure, whilst the processes of growth and secretion occur alike in both plants and animals. Accordingly the respiratory mechanism is much more highly organised in animals, simple diffusion being sufficient to provide for the requirements of plants. The respiratory process in animals will now be considered.

Respiratory Mechanism in Animals

In the mammal the lungs are filled (inspiration) and emptied (expiration) by the alternate increase and decrease in capacity of the thoracic

cavity, effected by the expansion and contraction of the rib cage and the lowering and raising of the diaphragm respectively. This mechanism may be demonstrated by the use of the apparatus shown in Fig. 259. As water is allowed to escape from the jar, air enters the balloon, which thus becomes inflated. If water is then introduced into the jar via the tube at its base, the additional pressure within the jar causes the balloon to become deflated.

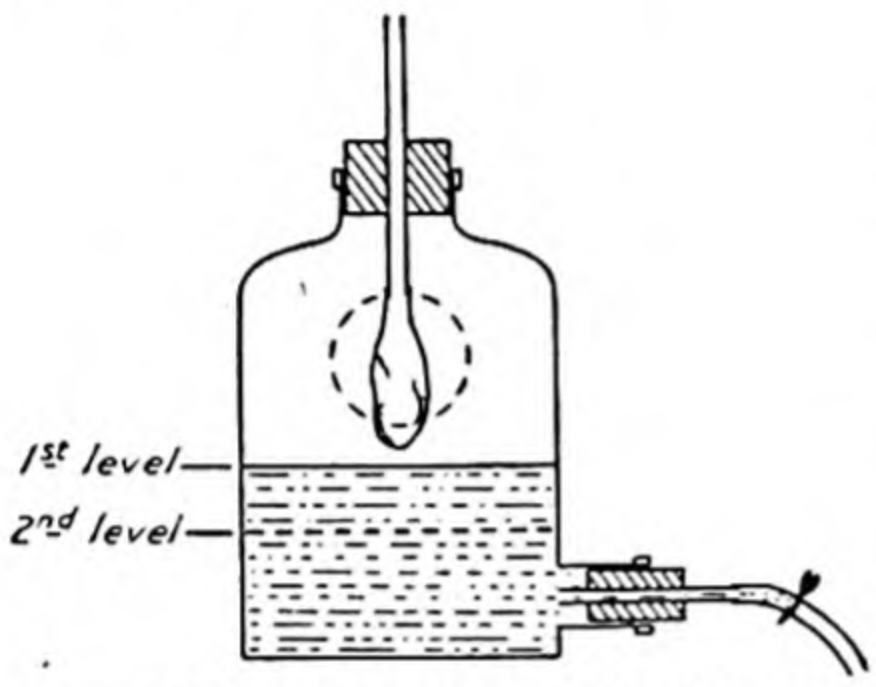


FIG. 259 – Apparatus for the demonstration of the principle governing the filling of the lungs of mammals.

In Man, the total capacity of the lungs is about $5\frac{1}{2}$ litres. The volume of air inspired (and expired) at a single, normal breath, known as the *tidal volume*, is between 500 and 600 ml, of which approximately 140 ml fills the dead space of the nasal passages, trachea, bronchi and bronchioles – i.e. it never reaches the air sacs and alveoli. Thus approximately 400 ml of fresh air enters the alveoli per breath, and here it encounters some $2\frac{1}{2}$ litres of stationary air already present in the alveoli – i.e. that which is not expelled in normal expiration. The function of inspired air, containing 21% oxygen and 0.03% carbon dioxide, is to maintain constant the composition of the stationary air, compensating for gaseous exchange with the blood. As a result of gaseous exchange between the inspired air and the stationary air, expired air contains 16.4% oxygen and 4.1% carbon dioxide. This marked change in composition may well be anticipated in view of the relatively large volume of stationary air.

It must be borne in mind that there is continuous gaseous exchange between some of the gases of the stationary air and those of the blood. Thus oxygen diffuses from the air into the blood, where it associates chemically with haemoglobin. The presence of this oxygen-carrier is essential, since oxygen is not sufficiently soluble in plasma alone to meet the respiratory needs of the animal. Carbon dioxide, returned from the working organs by the blood, diffuses simultaneously into the stationary air. This diffusion is facilitated by the very thin nature of the walls of the pulmonary capillaries and of the alveoli and air sacs. Dense networks of capillaries lie in intimate contact with the walls of the alveoli and air sacs, thus making diffusion readily possible.

A state of equilibrium is never attained, since the supply both of blood and air is being constantly renewed. This process of gaseous exchange at the lungs is known as *external* respiration.

Oxygen, having thus entered the blood, is carried about the body until

it reaches some organ requiring energy to do work. In such an organ the oxygen-content will be low, whilst a considerable quantity of carbon dioxide will be present. In consequence gaseous exchange, similar to that described as occurring in the lungs, takes place, oxygen being given

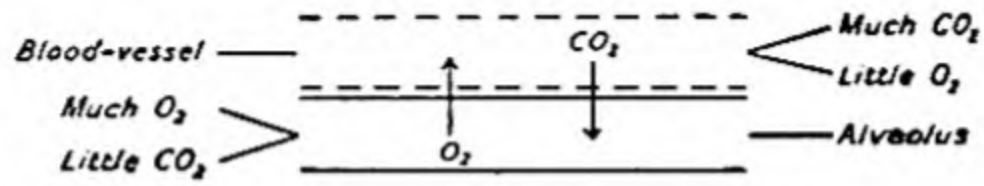


FIG. 260 – Diagram to illustrate the principle of gaseous exchange in the lungs of air-breathing vertebrates.

up to the tissues and carbon dioxide carried away in the blood. This gaseous exchange at the tissues, and subsequent oxidation, is termed *internal* respiration.

In the frog the mechanism of filling and emptying of the lungs is somewhat different. Inspiration is effected as follows. The mouth is first closed, the nares opened and the body of the hyoid lowered. This results in the passage of air into the buccal cavity, where a certain amount of gaseous exchange occurs through the moist mucous membrane. The nares are now closed by the upward movement of the premaxillae, whilst the hyoid body is raised. These movements result in the air's being forced into the lungs, the glottis being opened. Throughout both phases of the inspiratory process the oesophagus is kept closed by muscular contraction.

At expiration the reverse processes occur, the air being first drawn from the lungs by the lowering of the body of the hyoid. This phase is assisted by the elasticity of the lungs, due to the presence of strong bands of smooth muscle, and the contraction of the flank muscles. Air is then made to escape through the open nares, the glottis now being closed. The oesophagus is still maintained closed throughout. It should be borne in mind that the lungs still fulfil the primitive function of buoyancy organs (swim bladder) in the aquatic periods of the frog's life.

The skin also acts as an important respiratory surface. In fact, only during periods of activity (on land, of course) are the lungs used at all as respiratory organs. The pulsating movements of the floor of the buccal cavity of the resting frog are merely facilitating the ventilation of that cavity.

Fish make use of the oxygen dissolved in their water medium for the purpose of respiration. Water enters the buccal cavity and is forced through the gill-slits as a result of the raising of the floor of that cavity, a movement analogous to that occurring in Amphibia. During its passage over the lamellae of the gills the blood becomes oxygenated, whilst waste carbon dioxide is passed into the water and removed. In some fish, including *Scyliorhinus*, water enters also through the spiracles.

Many Invertebrata have no special respiratory mechanism, oxygen being absorbed through the surface, and carbon dioxide escaping in like

manner. In some forms – e.g., *Lumbricus* – this absorption of oxygen is followed by its distribution in the blood. But other invertebrates do possess special respiratory organs. The tracheae of insects have already been described (page 75). Their filling and emptying are effected principally by the movements of the abdomen, facilitated by special muscles, resulting in alternate compression and expansion of the tracheae. Mollusca – e.g., the garden snail and the fresh-water mussel – effect gaseous exchange through a delicate fold in the body-wall, known as the **mantle**. The so-called 'gills' of the mussel are largely concerned with nutrition.

Respiratory Mechanism in Plants

In higher plants air enters the leaves and young stems by the stomata, whilst lenticels in older stems and roots where cork has been laid down serve a similar function. Once within the plant the air is distributed through the intercellular spaces, the continuity of which may be demonstrated experimentally. A cut shoot of a plant is firmly attached by means of pressure tubing to a piece of glass tubing, bent as shown in Fig. 261.

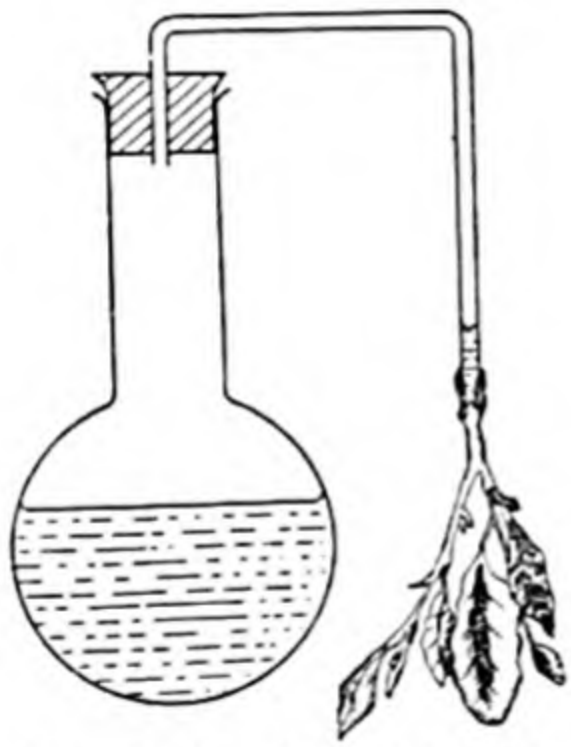


FIG. 261 – Apparatus for the demonstration of the continuity of air-spaces in a plant.

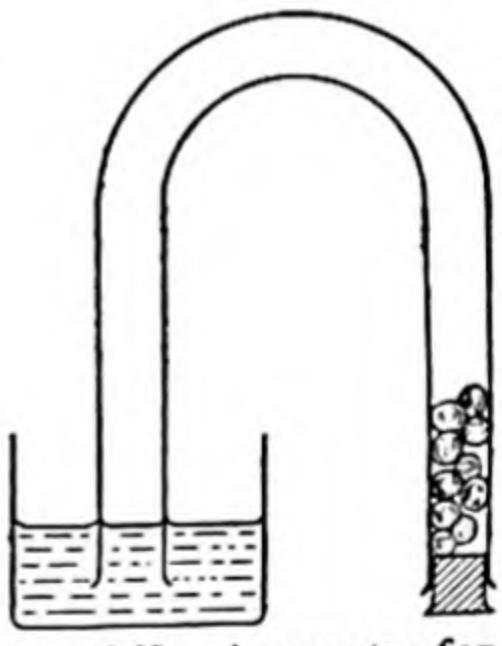


FIG. 262 – Apparatus for the demonstration of the necessity of oxygen for germination.

Above the cut tip of the shoot is introduced a small quantity of water, whilst the whole surface of the shoot, with the exception of the leaves, is vaselined to prevent the escape of air. Water is then boiled in the round-bottomed flash, and when the latter is full of steam the stopper carrying the glass tube is pressed in tightly. As the steam condenses a reduction in pressure results, and bubbles of air may be seen to rise from the cut end of the shoot. Thus air is distributed from one part of the plant to another simply by diffusion.

That oxygen is necessary for life and growth of a plant may be shown with soaked peas. The latter are placed in a U-tube, one limb of which is

then tightly corked. The U-tube is then inverted so that the peas rest on the cork, whilst the mouth of the open limb is inserted into an alkaline solution of pyrogallol, a powerful absorbent of oxygen. A control experiment is arranged, identical with the above except that the pyrogallol is replaced by water. In the latter the seeds germinate, whilst those robbed of their oxygen fail to do so.

The evolution of carbon dioxide during respiration by the green plant can be demonstrated only if the plant is retained in darkness; otherwise the results will be masked by the occurrence of photosynthesis. The apparatus shown in Fig. 263 is employed. The selected plant is retained

FIG. 263 – Apparatus for the demonstration of the evolution of carbon dioxide by a green plant in darkness.

beneath the bell-jar, admission of air being largely prevented by the greasing of the glass plate upon which the bell-jar rests. Air is drawn successively through a tube containing soda-lime to extract atmospheric carbon dioxide, and a wash-bottle containing lime-water, to prove that extraction has been completed. After passage through the compartment containing the plant the air passes through further quantities of lime-water, and it is found that this turns milky, thus proving that the plant has evolved carbon dioxide. A control experiment is carried out with identical apparatus, except that no plant is placed beneath the bell-jar, but a pot containing soil is included, showing that the carbon dioxide cannot come from this source.

The amount of carbon dioxide evolved by germinating seeds may be fairly readily estimated. The apparatus required is shown in Fig. 264. Flask *A* contains a concentrated solution of sodium hydroxide for the removal of atmospheric carbon dioxide, and its efficacy is tested by lime-water contained in flask *B*. In flask *C* are the germinating seeds. In bulbs *D* is placed 100 c.c. of $\frac{N}{40}$ baryta water. The delivery tube from bulbs *D* is connected to a filter-pump, so that air may be drawn slowly through the whole apparatus. The rate of flow should be so regulated that about 60 bubbles pass through per minute. At the end of a given period – e.g., six hours – the baryta water from bulbs *D* is carefully washed with carbon dioxide-free water into a large conical flask, two drops of phenolphthalein added, and the excess baryta titrated against

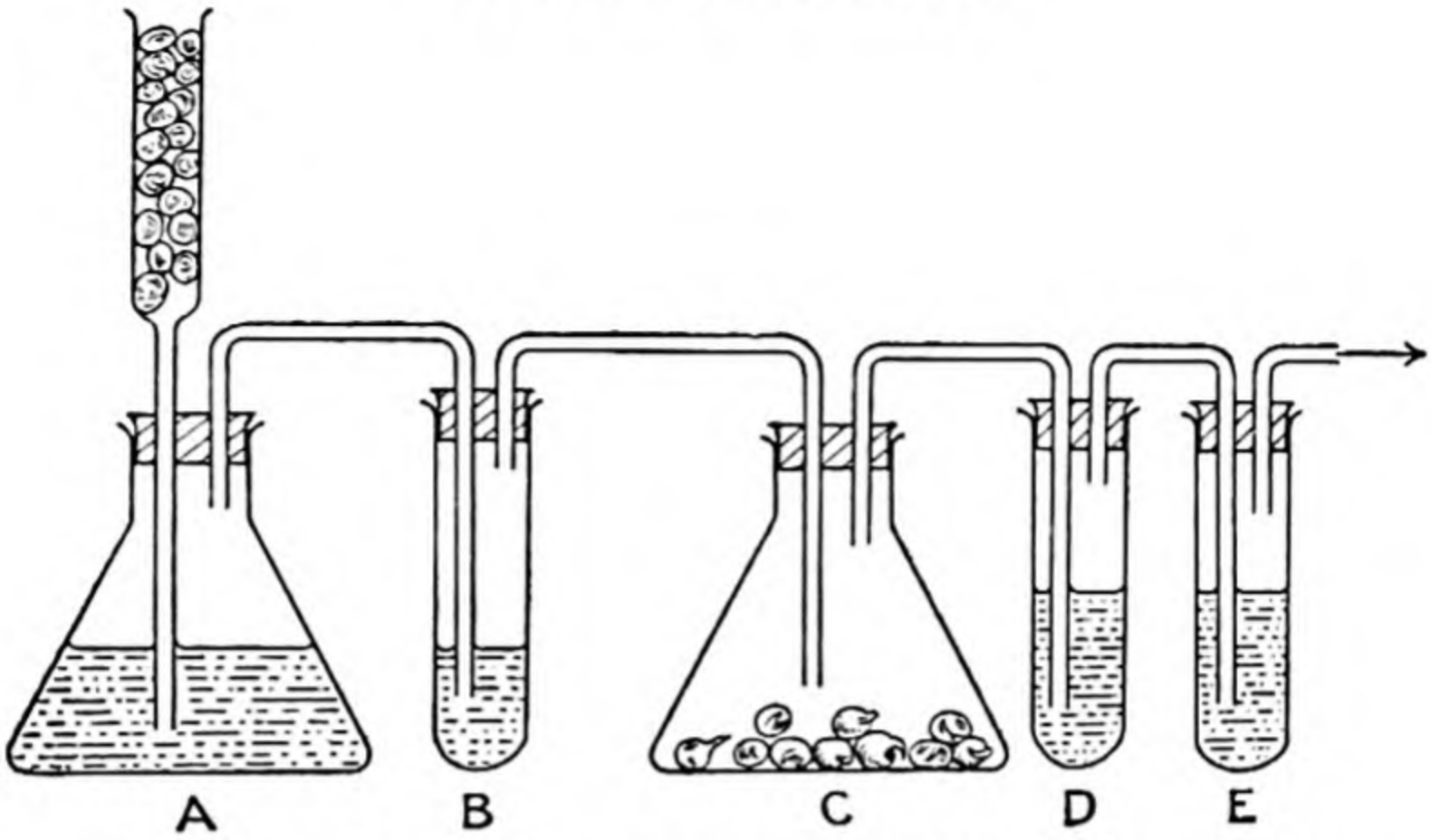


FIG. 264 – Apparatus for the measurement of the rate of respiration of germinating seeds. For description see text.

$\frac{10}{N}$ hydrochloric acid. Having thus obtained a measure of the excess baryta, the amount neutralised by the carbon dioxide can be determined, and hence the weight, and if necessary the volume, of carbon dioxide evolved may be calculated.

The amount of carbon dioxide evolved is regarded as a fairly reliable index of the rate of respiration. The latter will obviously depend on a number of conditions within the plant, and thus will vary at different

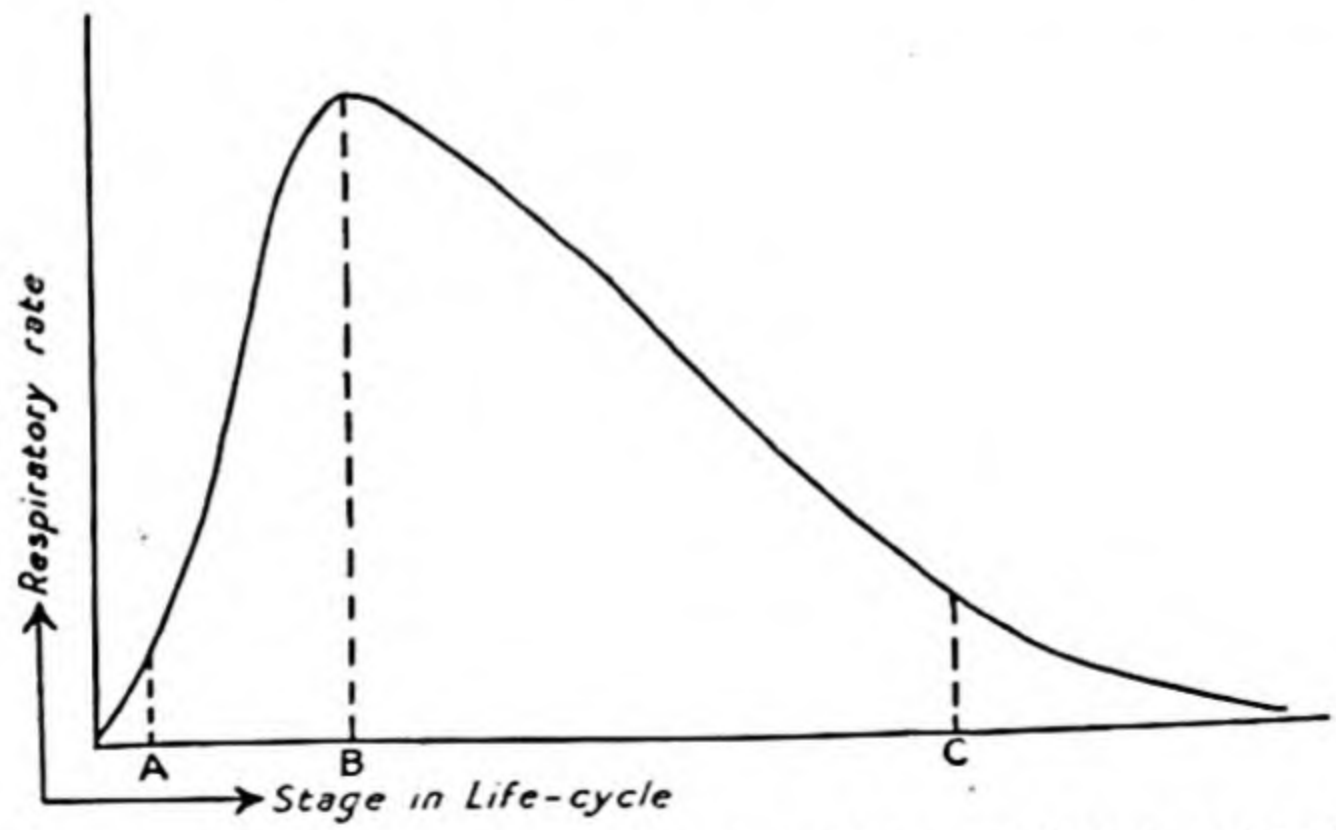


FIG. 265 – Graph to demonstrate the relative respiratory rates at various stages in the life-history of a seed plant.
A., The outset of germination; *B.*, Later germination; *C.*, Approaching fruit- and seed-formation.

stages in the life-cycle. It is found to show a progressive decline from its comparatively high rate in embryonic tissues, e.g., meristems and germinating seeds, through mature tissues, such as functional leaves, and senescent tissues, e.g., ripening fruits, to an almost complete cessation in dormant tissues, as exemplified by dry seeds. Thus, if the respiratory index is calculated as the percentage weight of carbon dioxide evolved per gram of dry weight, the respiratory rate throughout the life-cycle of a plant may be represented graphically as in Fig. 265.

Chemistry of Respiration

Before proceeding to a consideration of the chemistry of respiration it will be well first to become clear about the problem presented. It must be understood that protoplasm as a whole is not, as formerly held, undergoing continuous oxidation. If this were so the amount of nitrogenous waste matter would necessarily be very much greater than it is. It is true, however, that certain of the simpler nitrogenous substances – e.g., amino-acids – in animals do undergo oxidation, but this occurs in plants only in the last stages of starvation. But the products of respiration are carbon dioxide and water, and they are formed by the oxidation of sugars present, as suggested in the following equation:

$$C_6H_{12}O_6 + 6O_2 = 6CO_2 + 6H_2O + 674 \text{ kilocalories.}$$

But a reaction of this complexity cannot be expected to take place in a single step, and the equation must be regarded merely as a convenient summary of the process. Basically the entire process is divisible into two phases, which will be considered in turn.

GLYCOLYSIS. This is the breaking down of glucose into two smaller units, each containing three carbon atoms. Its performance is independent of the presence of oxygen, energy being derived from *A.T.P.* (see page 436). The primary reaction is primed by the enzyme *hexokinase*, working in the presence of magnesium ions, and results in the formation of glucose-6-phosphate. Thus –

$$\text{Glucose} + A.T.P. \xrightarrow[Mg^{++}]{Hexokinase} \text{Glucose-6-phosphate} + A.D.P.$$

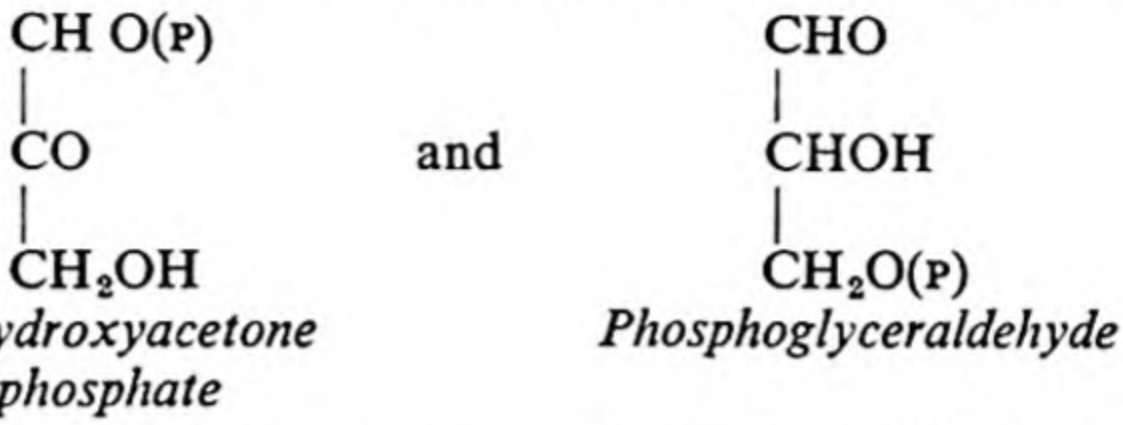
In the presence of a specific *isomerase*, this latter compound is then converted into fructose-6-phosphate. Thus –

$$\text{Glucose–6–phosphate} \xrightarrow{Isomerase} \text{Fructose-6-phosphate}$$

In the presence of the enzyme *phosphohexokinase*, again in the presence of magnesium ions and with energy derived from *A.T.P.*, this compound is next converted into fructose-1:6-diphosphate. Thus –

Fructose-6-phosphate + *A.T.P.* $\xrightarrow[Mg^{++}]{\textit{Phosphohexokinase}}$ Fructose-1:6-diphosphate + *A.D.P.*

At this point there is a split of the molecule, under the influence of the enzyme *aldolase*, into two molecules of triose phosphate, namely

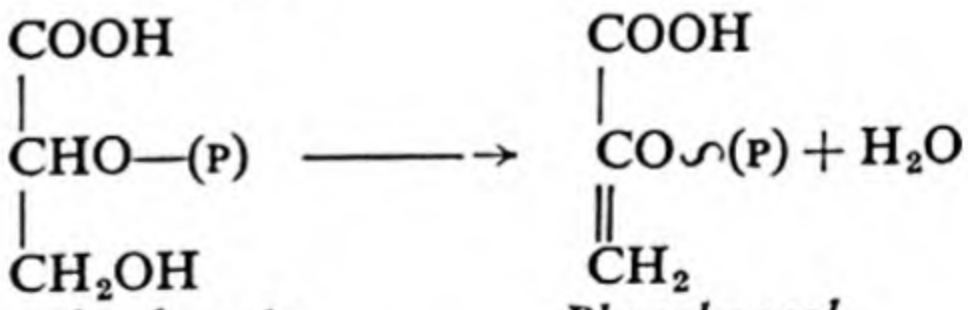


Dihydroxyacetone phosphate and *Phosphoglyceraldehyde*

Although the former is in greater quantity in the equilibrium mixture, it is the latter compound which is involved in the next stage. As it is utilised more of it is formed from the dihydroxyacetone phosphate, aided by the enzyme *triosephosphate isomerase*. The phosphoglyceraldehyde is, in fact, oxidised by the removal of two atoms of hydrogen (enzyme *triose dehydrogenase*), simultaneously condensing with a molecule of phosphoric acid to form 1:3-diphosphoglyceric acid. This compound eventually decomposes with the formation of more *A.T.P.* Thus –

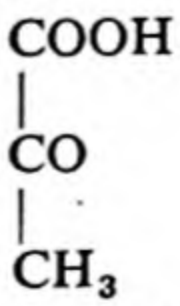
1:3-diphosophoglyceric acid + *A.D.P.* → 3-phosphoglyceric acid + *A.T.P.*

Under the influence of *phosphoglyceromutase*, this latter compound is converted into the corresponding 2-isomer which, by the loss of water and in the presence of the enzyme *enolase* and magnesium ions, becomes phosphoenolpyruvic acid. Thus –



2-phosphoglyceric acid *Phosphoenol-pyruvic acid*

With the liberation of an energy-rich phosphate bond, this is now converted into pyruvic acid, of formula –



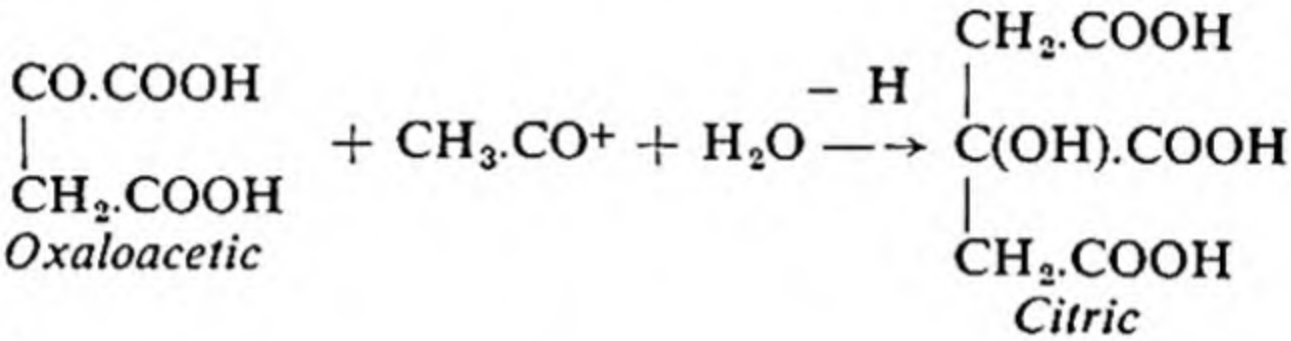
The fate of this pyruvic acid depends upon the availability of oxygen. In the presence of adequate supplies of this element, direct oxidation to

carbon dioxide occurs. Otherwise, the pyruvic acid may itself act as an oxidising agent, being reduced to lactic acid. Thus –

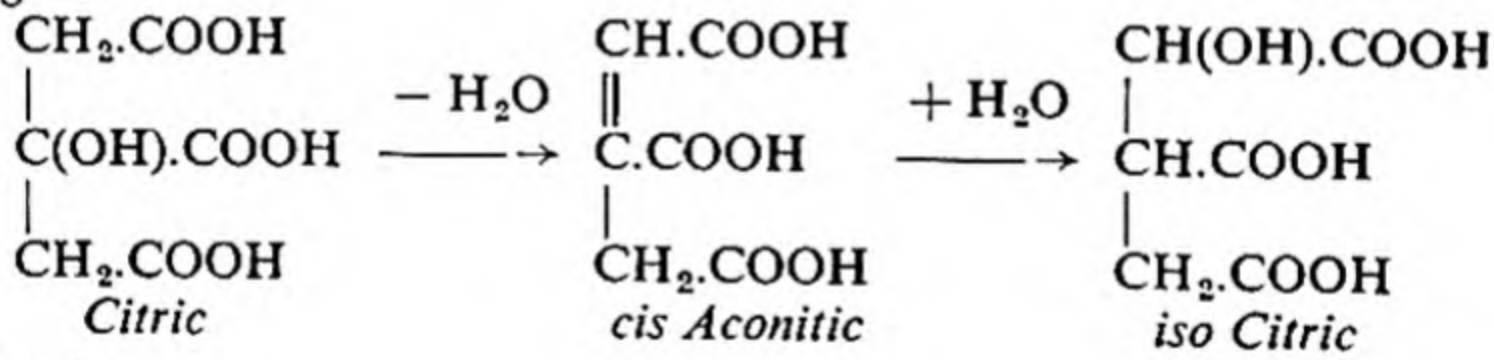
$$CH_3CO.COOH + 2H \rightarrow CH_3.CHOH.COOH$$

THE TRICARBOXYLIC ACID CYCLE. Regarding pyruvic acid (or the pyruvate ion) as the natural end-product of glycolysis, it has been found that its subsequent fate is linked with a complex series of reactions, known as the *Tricarboxylic Acid Cycle* (alternatively known as the *TCA*, *Citric Acid*, or *Krebs*, *Cycle*). This is prefaced by a peculiar oxidative decarboxylation of the pyruvic acid, resulting in the formation of a highly reactive acetyl group and achieved with the co-operation of numerous enzymes and co-enzymes. This acetyl group, in its turn, reacts with oxaloacetic acid, itself an intermediate metabolite in the oxidation of pyruvic acid, resulting in the formation of citric acid. The events of the TCA cycle may thus be summarised as follows –

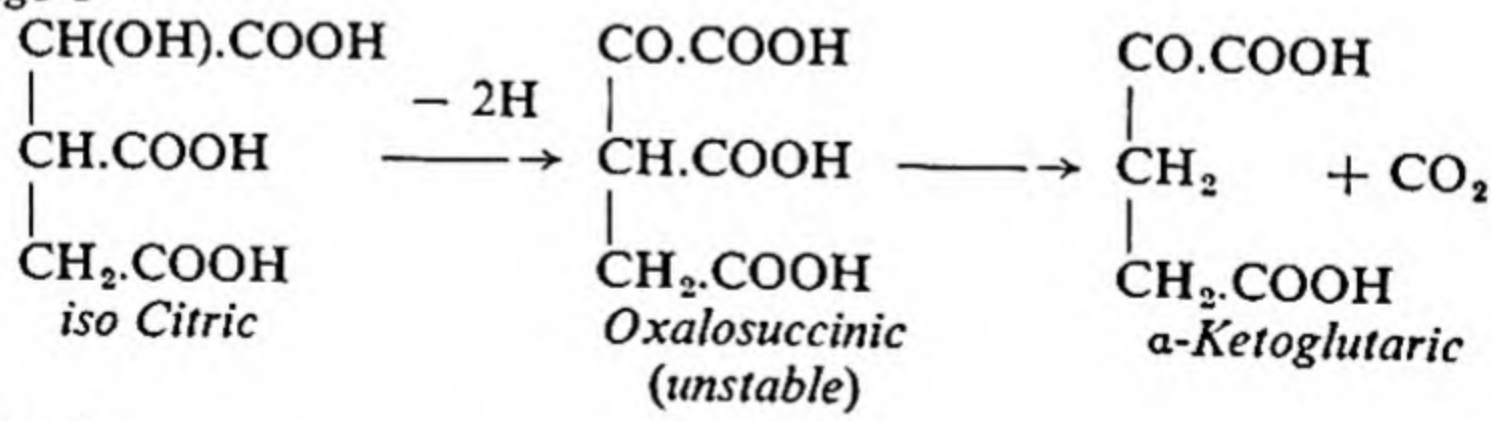
Stage 1



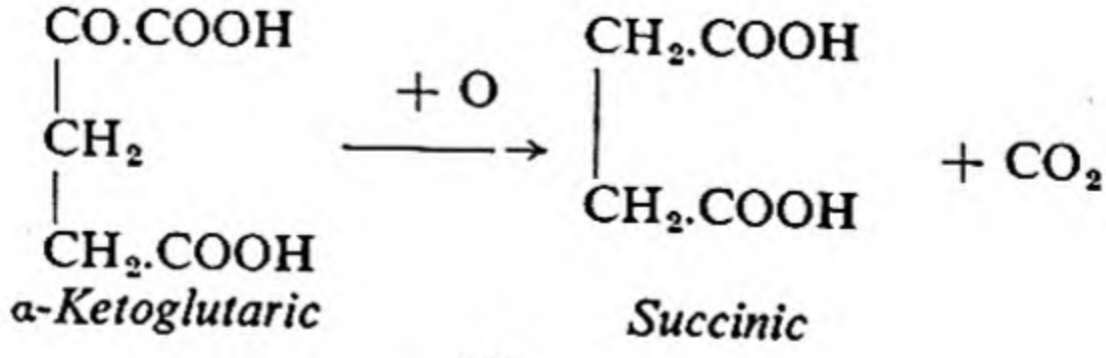
Stage 2



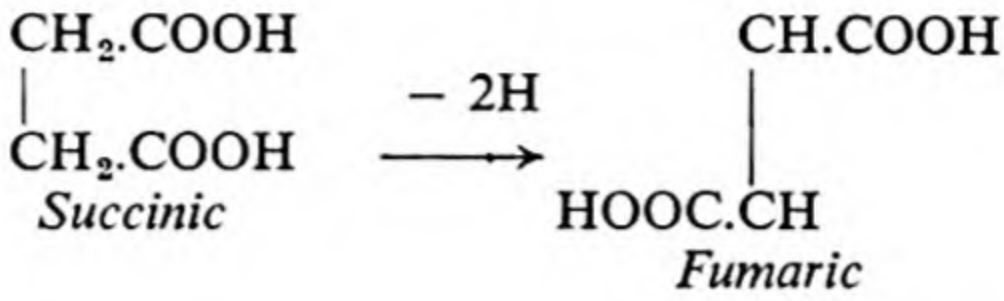
Stage 3



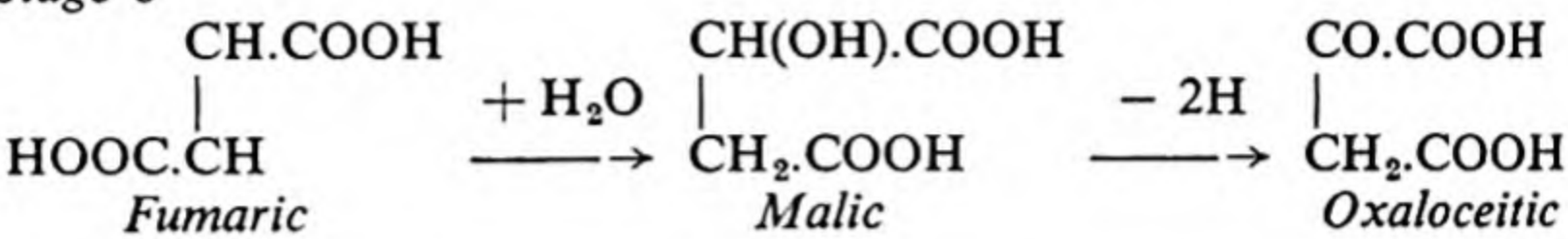
Stage 4



Stage 5



Stage 6



Thus, each time the cycle is completed, two molecules of carbon dioxide are formed as a result of oxidation (stages 3 and 4) and eliminated. This takes place as a result of the decomposition of water to yield the necessary oxygen, involving the removal of hydrogen from the system, a process assisted by dehydrogenases. This hydrogen is acquired by the specific hydrogen-carriers, di- and tri-phosphopyridene nucleotide (*D.P.N.* and *T.P.N.*) and transferred through various other hydrogen-acceptors, ultimately to oxygen. The oxidation of hydrogen to water yields the energy associated with metabolism. This latter function is largely the function of the cytochrome system (see below), for, with the aid of these respiratory catalysts, electrons are transferred from organic hydrogen to oxygen, thus bringing about the oxidation of hydrogen to water.

OXIDATION CATALYSTS. Most of the substrates used in biological oxidation for the liberation of energy do not combine directly with atmospheric oxygen. Catalysts, collectively termed *enzymes* and *coenzymes*, are required. Respiratory enzymes are classified according to the type of oxidation which they assist. As was seen in some of the reactions quoted above, oxidation is often achieved in the living organism by dehydrogenation. The enzymes which facilitate such reactions are termed **dehydrogenases**. But the fate of the removed hydrogen must also be taken into account. It is often handed on from one hydrogen-carrier to another before itself undergoing oxidation to form water. Such carriers are *coenzymes*. The following hypothetical example, involving the oxidation of the substrate AH_2, by dehydrogenation, will make this clear. Thus –

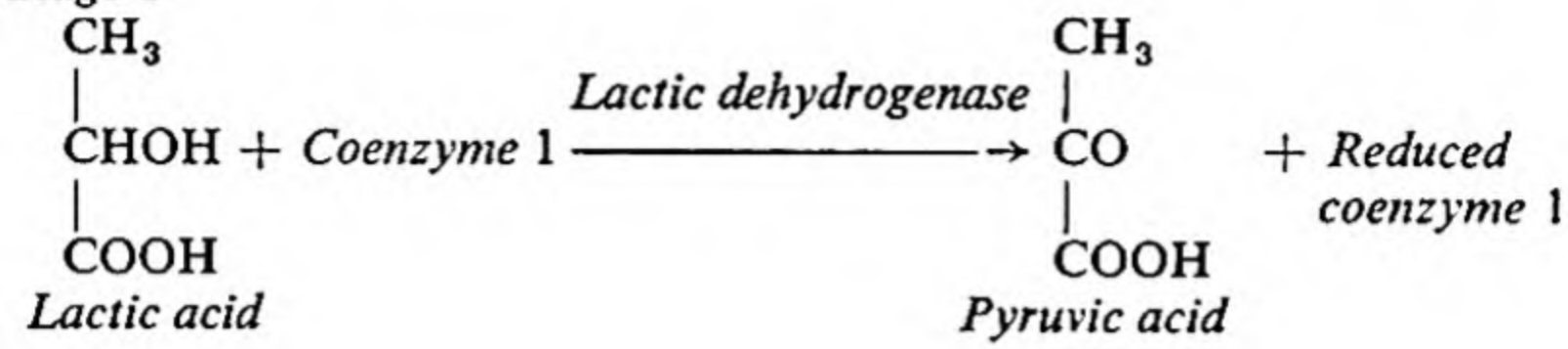
Stage 1. $AH_2 + X \rightarrow A + XH_2$
Stage 2. $XH_2 + Y \rightarrow X + YH_2$
Stage 3. $YH_2 + O \rightarrow Y + H_2O$

Each of the stages is itself catalysed by an enzyme. For the oxidation of AH_2 to A and water, X and Y are coenzymes.

A particular instance of the generalised sequence of reactions quoted

above is provided by the oxidation of lactic acid to pyruvic acid. Thus –

Stage 1



Stage 2

$$\textit{Reduced coenzyme 1} + \textit{Cytochrome c} \xrightarrow[\textit{dehydrogenase}]{\textit{Coenzyme 1}} \textit{Coenzyme 1} + \textit{Reduced cytochrome c}$$

Stage 3

$$\textit{Reduced cytochrome c} + O_2 \xrightarrow[\textit{oxidase}]{\textit{Cytochrome}} \textit{Cytochrome c} + H_2O$$

The cytochromes, of which at least four are known (styled *a*, *b*, *c* and *f*,) are important respiratory catalysts, at least one of the forms being present in all tissues (animal and plant) capable of aerobic respiration. Cytochrome *c* is the best known, whilst cytochrome *f* is peculiar to green plants, functioning in the conditions obtaining within tissues capable of photosynthesis. As is clear from the above example, they are able to receive hydrogen from substrates, after which, in the presence of appropriate cytochrome oxidases, they themselves become converted to the free form. A molecule of cytochrome may become reduced and oxidised at a rate of some 2,000 times per minute. Their efficiency depends largely upon their concentration upon cell particles, such as mitochondria. They are highly complex compounds, not unlike haemoglobin in chemical composition. There is one atom of iron per molecule and this oscillates between the ferrous and ferric states.

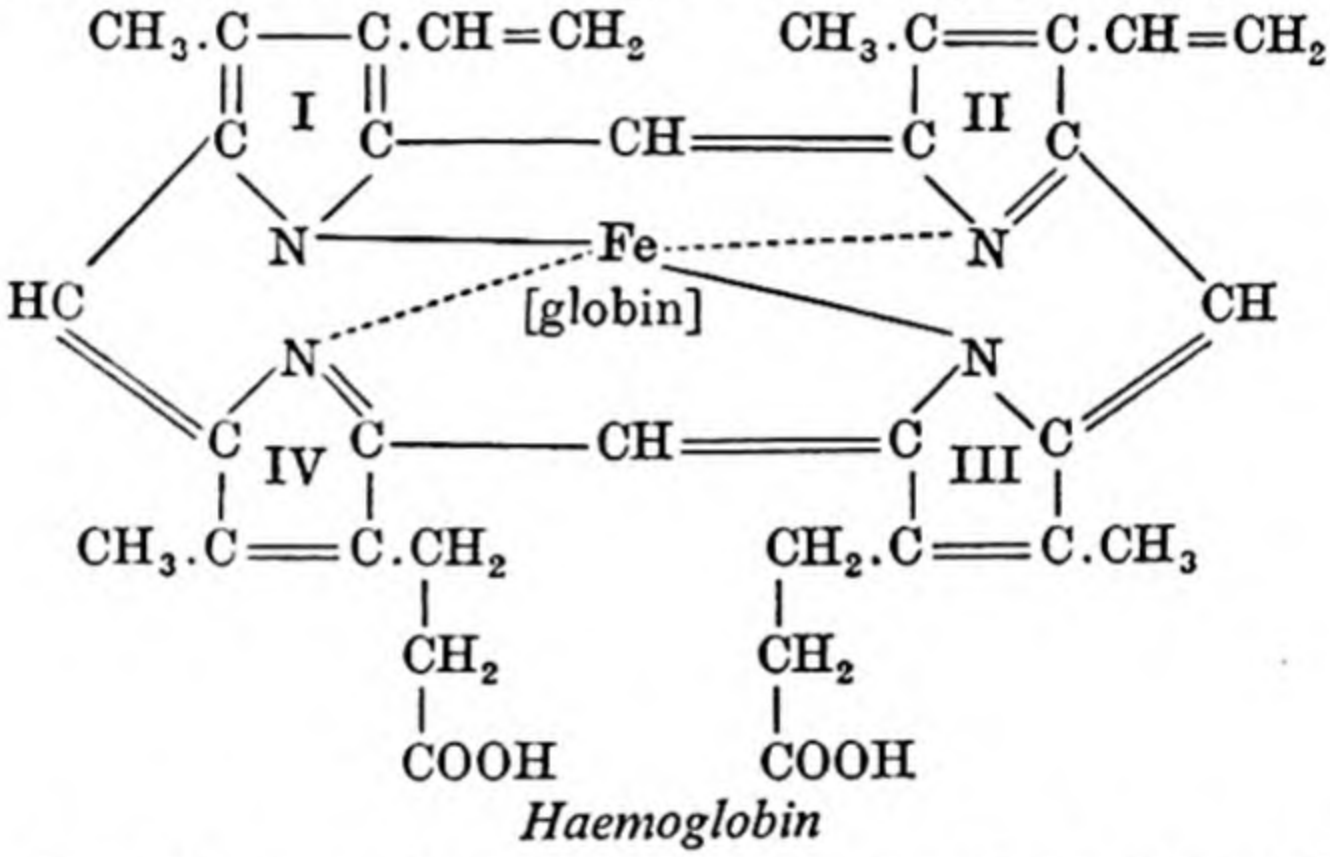
Whereas dehydrogenases facilitate the loss of hydrogen, **oxidases** assist direct union with oxygen. Examples are provided by tyrosinase, responsible for catalysing the oxidation of the amino-acid, tryosine, to the characteristic pigment, melanin. Its absence from the metabolic system causes albinism. Polyphenol oxidase accelerates the browning of the surface of cut apples.

Hydrogen peroxide is occasionally formed as an intermediate product in oxidative metabolism. Its decomposition is catalysed by enzymes termed **peroxidases.**

Coenzymes work in conjunction with enzymes, as stated above.

Inorganic ions – e.g. magnesium – may act in this capacity. Ascorbic acid (vitamin *C*) is a coenzyme with strong reductive potentialities. Diphosphopyridene nucleotide (*D.P.N.*) is an important coenzyme. Known also as a coenzyme 1, it is a highly efficient hydrogen-acceptor. Reference to its activity in the TCA cycle has already been made (page 432).

It will be apparent from the above that **cytochromes**, of which several are known to exist, are of very great importance in biological oxidation systems. In fact these compounds are present in the tissues of all organisms which depend upon molecular oxygen for respiration. To some extent they resemble **haemoglobin**, the respiratory pigment of the



Haemoglobin

blood of vertebrates and of some invertebrates. The presence of such a respiratory pigment is necessary on account of the low solubility of oxygen. In fact, haemoglobin increases the oxygen-carrying capacity of the blood about sixty times. Structurally haemoglobin is a complex of two molecules – a *haem* molecule, with an iron atom (ferrous) at its centre, attached to a large *globin* molecule, of protein nature. When oxygen is brought into contact with haemoglobin a loose compound, known as oxyhaemoglobin, is formed, and in this way oxygen is transported from the respiratory organs to various parts of the body. But the iron present in haemoglobin remains ferrous, so that oxygenation, rather than oxidation, may be said to have occurred. At the tissues the oxygen is given up, resulting in the liberation of haemoglobin. But the iron in cytochrome undergoes an actual valency change. Thus in reduced cytochrome it is present as ferrous iron, whilst in the oxidised products it is ferric. Thus true oxidation and reduction occur. These facts may be summarised as follows:

$$\text{Fe}^{\cdot\cdot}\text{ haemoglobin} + \text{O}_2 \underset{\textit{de-oxygenation}}{\overset{\textit{oxygenation}}{\rightleftharpoons\!=\!=\!=\!=\!=\!=\!=\!\rightleftharpoons}} \text{Fe}^{\cdot\cdot}\text{ oxyhaemoglobin}$$

$$4Fe^{\cdot\cdot}\text{ (reduced) cytochrome} + O_2 \underset{\text{reduction}}{\overset{\text{oxidation}}{\rightleftharpoons\!=\!=\!=\!=\!\rightleftharpoons}} 4Fe^{\cdot\cdot\cdot}\text{ cytochrome} + 2H_2O$$

Anaerobic Respiration

So far only such respiration as depends on the presence of atmospheric oxygen has been considered. But many micro-organisms respire in the absence of molecular oxygen, which indeed may be actually fatal to them. Such respiration is described as **anaerobic**. Not only so, but plants in general seem to be capable of respiring anaerobically for considerable periods if deprived of their normal supply of oxygen. This may be demonstrated with germinating peas. The outer coats of soaked peas are removed, thereby eliminating the possibility of air being enclosed. A test-tube containing mercury is then inverted in a trough of mercury, and the peas are introduced into the mouth of the tube. They rise to the top, and after a short time it becomes evident that a gas is being evolved. If left for some twenty-four hours sufficient gas may be formed to fill the tube. If a small piece of caustic soda is now introduced into the tube the gas is absorbed, showing that it is carbon dioxide. This means of necessity that some sort of oxidation has been taking place, but the oxidant must be some constituent of the cells, since there is no access to atmospheric oxygen. In its main features fermentation of sugars by yeast is similar to anaerobic respiration by higher plants, the similarity extending to the products formed, and possibly also to the mechanism employed. The chief end-product of such fermentation is ethyl alcohol, whilst carbon dioxide is evolved. The reaction may be approximately summarised by the following equation:

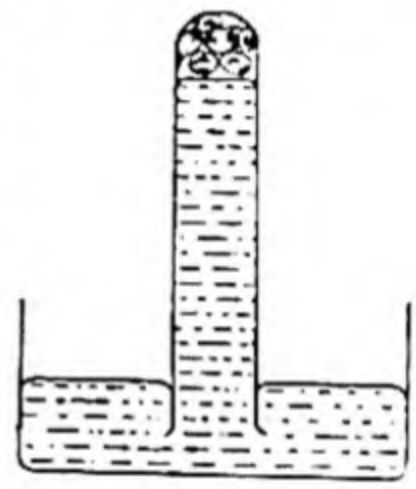


FIG. 266 – Apparatus for the demonstration of anaerobic respiration in seeds.

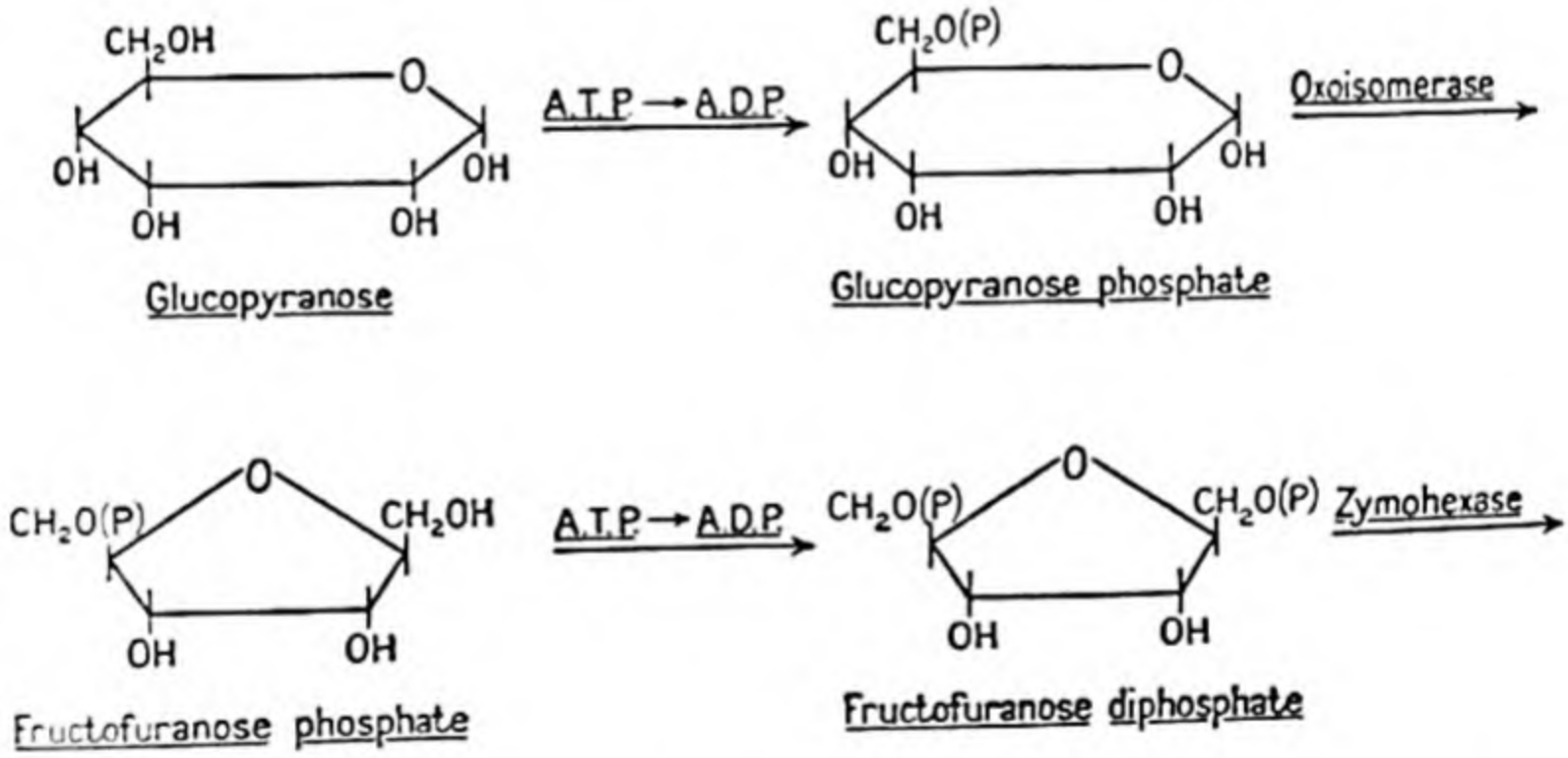
$$C_6H_{12}O_6 = 2\,C_2H_5OH + 2\,CO_2 + 25 \text{ kilocalories.}$$

Yeast, a colourless Fungus, possesses to an unusual degree the ability to bring about fermentation (see below), and this property affords the basis of the manufacture of alcohol. It is essentially an enzyme action, being promoted by a complex of enzymes, collectively termed **zymase**. Fermentation of sugars by yeast appears to differ from anaerobic respiration by higher plant in one respect, and that is that the fermentation continues even in the presence of oxygen. Though able to withstand considerable periods of oxygen-starvation, this gas is eventually essential for the maintenance of life in the yeast cells. Further, only three hexose sugars amongst all carbohydrates are directly fermentable, and such yeast species as will ferment other sugars must needs first hydrolyse them into one of these three forms.

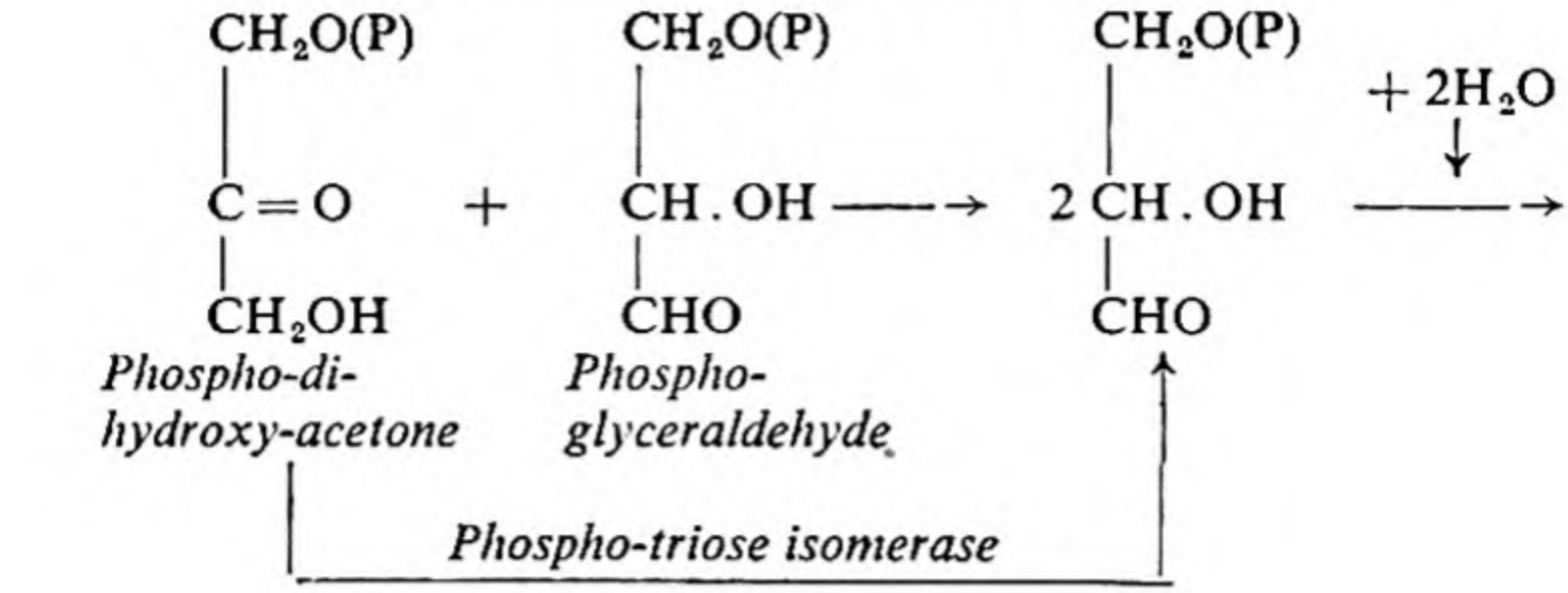
Chemistry of Anaerobic Respiration

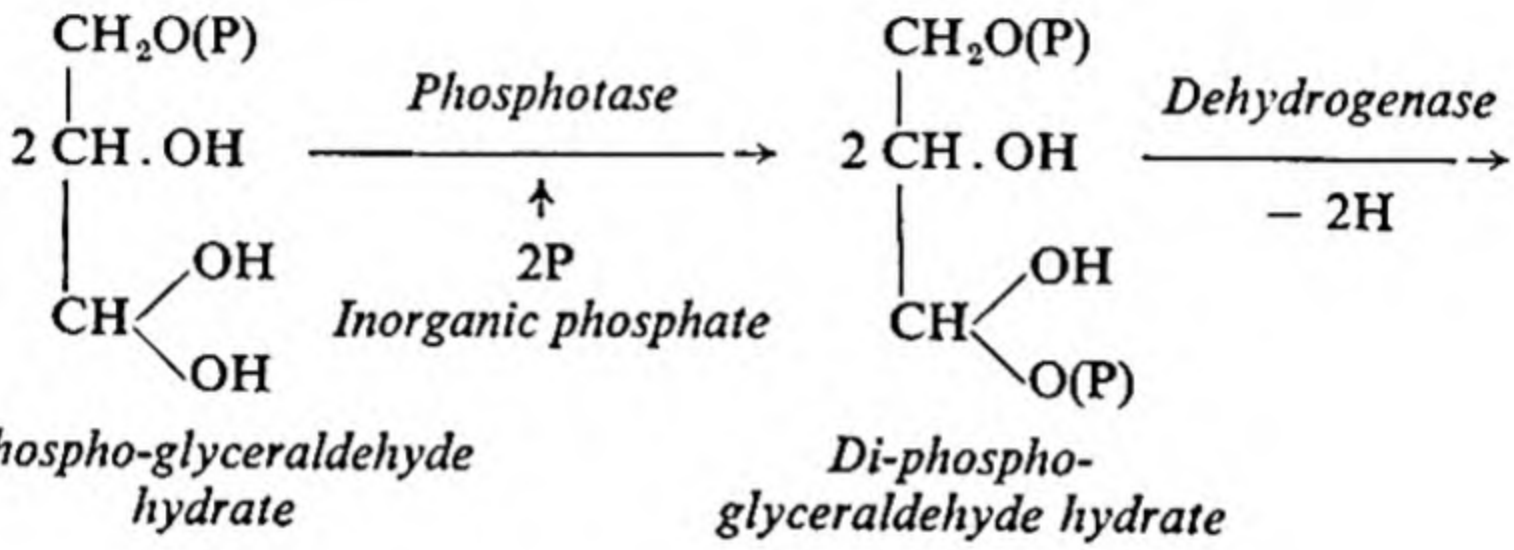
As well as ethyl alcohol a number of other products are formed as a result of fermentation, their relative quantities being to some extent regulated by experimental conditions. Amongst the more important may be mentioned glycerol, pyruvic acid and acetaldehyde. Various enzymes are involved in the process, and a possible sequence of reactions is indicated below. The phosphate ion plays a very important part, and the gain or loss of this ion by the substrate is largely governed by the two mutually interchangeable co-enzymes, known as *A.T.P.* (adenosine triphosphate) and *A.D.P.* (adenosine diphosphate) respectively. The former (*A.T.P.*) contains two high-energy phosphate bonds and one low-energy phosphate bond, whereas *A.D.P.* contains one bond of each kind. The transfer of high-energy phosphate bonds commonly provides means of energy transfer in metabolism.

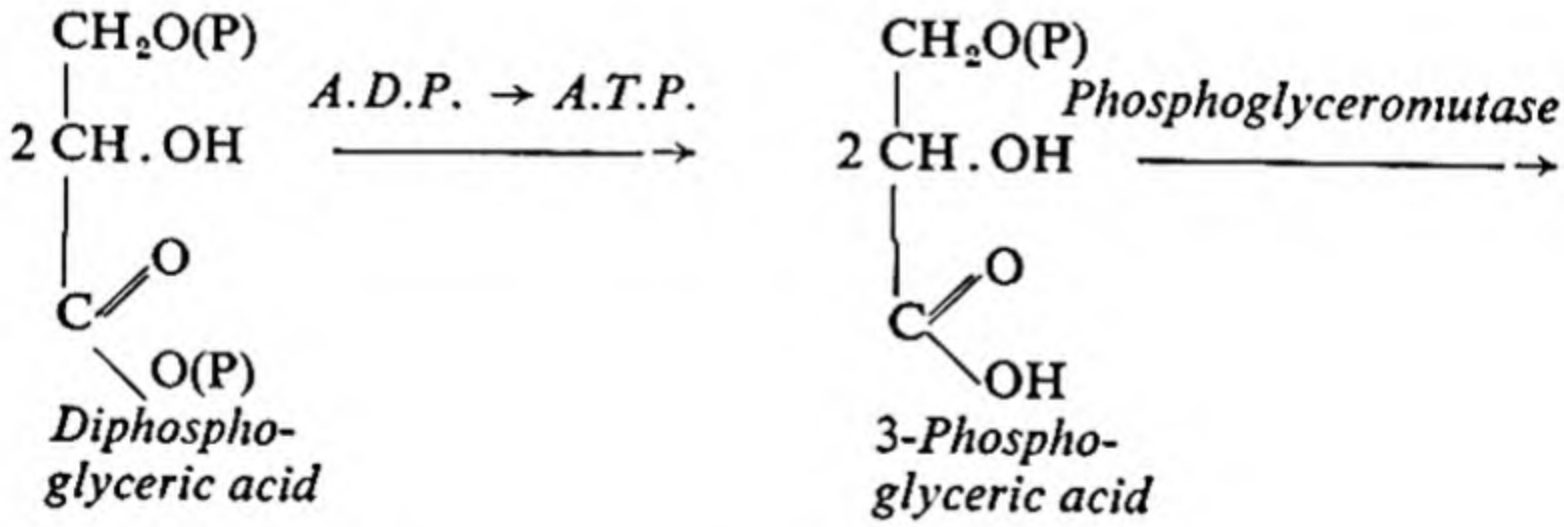
It will be at once apparent that, as far as the formation of pyruvic acid, the sequence of events set out below is identical with that constituting the glycolytic phase of aerobic respiration – i.e. the two mechanisms cover much common ground. To avoid the distraction of continual back-

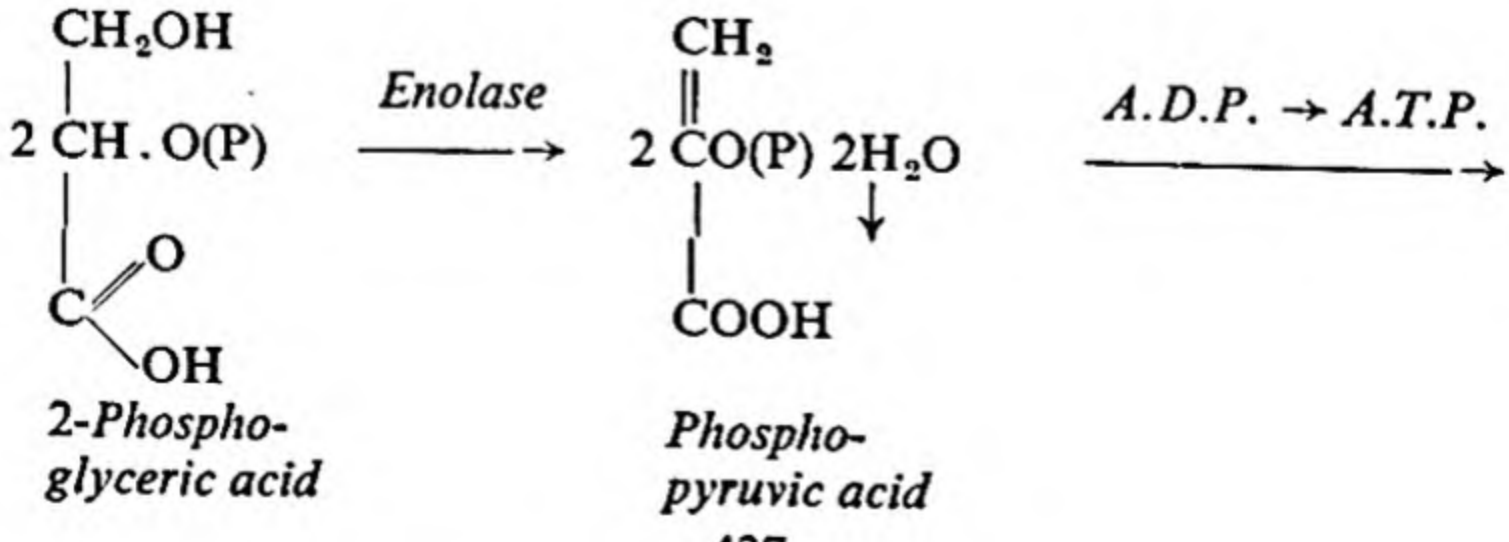


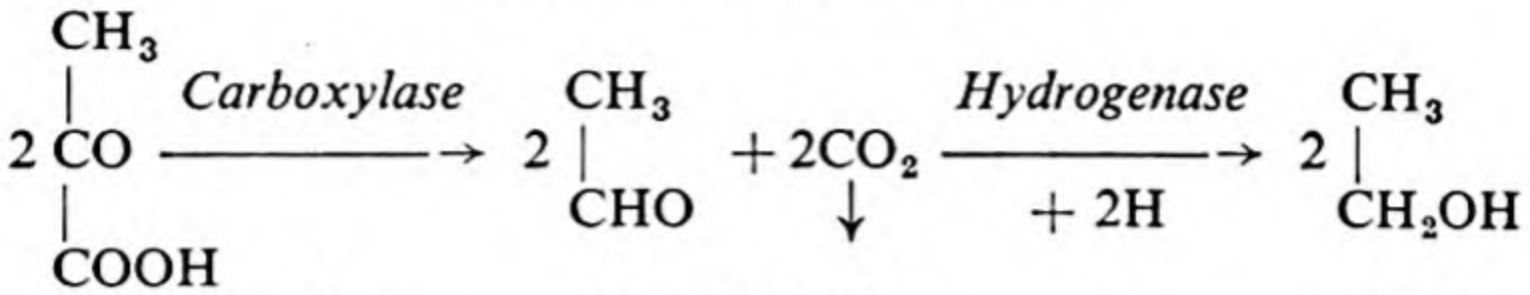
reference, the cycle is reiterated here, though in rather more abbreviated form in the initial stages. Alternative terms are used in some cases (e.g. glucopyranose phosphate is identical with the compound referred to as glucose-6-phosphate on page 429). It may be of value to students who wish to indulge in further reading on this topic to have encountered the two schemes of nomenclature.


CH2O(P)
C=O
CH2OH
+
CH2O(P)
CH.OH
CHO
CH2O(P)
2 CH.OH
CHO
+ 2H2O
Phospho-di-hydroxy-acetone
Phospho-glyceraldehyde
Phospho-triose isomerase


CH2O(P)
2 CH.OH
CH
OH
OH
Phosphotase
2P
Inorganic phosphate
CH2O(P)
2 CH.OH
CH
OH
O(P)
Dehydrogenase
− 2H
Phospho-glyceraldehyde hydrate
Di-phospho-glyceraldehyde hydrate


CH2O(P)
2 CH.OH
C
O
O(P)
A.D.P. → A.T.P.
CH2O(P)
2 CH.OH
C
O
OH
Phosphoglyceromutase
Diphospho-glyceric acid
3-Phospho-glyceric acid


CH2OH
2 CH.O(P)
C
O
OH
Enolase
CH2
2 CO(P)
COOH
2H2O
A.D.P. → A.T.P.
2-Phospho-glyceric acid
Phospho-pyruvic acid



Pyruvic acid *Acetaldeyhyde* *Ethyl alcohol*

It will be noted that during the process, two molecules of *A.T.P.* are de-phosphorylated to form *A.D.P.*, resulting in the liberation of considerable quantities of energy. But these molecules of *A.T.P.* are restored by the introduction of inorganic phosphate, and no doubt in these molecules a considerable quantity of the energy evolved in the various reactions is stored for subsequent metabolic use, whilst the remainder is liberated as heat.

The biological significance of fermentation, as of anaerobic respiration in general, is that it results in the liberation of energy, the characteristic feature of all cellular respiration. Though the vast majority of animals depend on a continuous supply of oxygen, a few normally carry out their vital processes without it. Thus gut-parasites, for example, usually respire anaerobically. Accordingly it is found that they store up considerable quantities of glycogen, so much so that 30% of the dry weight of *Ascaris* (Roundworm) and over 50% of that of the tapeworm consists of this substance. The glycogen is converted first into glucose, which is subsequently decomposed, yielding valeric acid (C_4H_9.COOH), hydrogen and carbon dioxide.

PRACTICAL WORK

Evolution of heat by Germinating Seeds

Place some barley seeds on moist blotting paper lining a funnel, as shown in Fig. 267. Into the germinating seeds insert the bulb of a thermometer. Caustic potash is used to remove carbon dioxide, which may otherwise interfere with the respiratory process of the seeds. Set up a second identical piece of apparatus, though the seeds used in this case must be killed by boiling, and sterilised by immersion in a solution of mercuric chloride, so as to prevent a rise in temperature as a result of bacterial decay. Note the temperatures carefully at the commencement and subsequently at regular intervals. The production of heat by the germinating seeds is the outcome of respiration. Thermos flasks may well be used as containers for the seeds in this experiment.

Evolution of Carbon Dioxide by Germinating Seeds

Set up the apparatus shown in Fig. 268, using soaked peas supported on lightly-packed, wet blotting-paper. A control experiment is provided

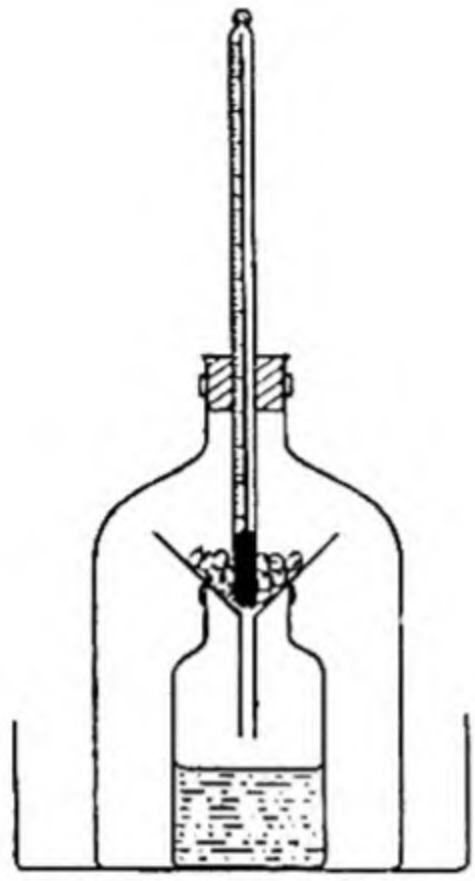


FIG. 267 – Apparatus for the demonstration of the evolution of heat by germinating seeds.

FIG. 268 – Apparatus for the demonstration of the evolution of carbon dioxide by germinating seeds.

by a similar piece of apparatus but without the tube of caustic potash. In the presence of caustic potash the level of water in the stem of the tap-funnel is observed to rise. This is due to the removal of oxygen and its replacement by carbon dioxide by the germinating seeds in the process of respiration, the carbon dioxide being absorbed by the potash. In the control experiment no such rise in level is observed.

Preparation of Alcohol by Fermentation

Into a large, round-bottomed flask place 10 grams of glucose dissolved in 200 c.c. of water. Add about an ounce of brewers' yeast. Fit a stopper into the flask, carrying a delivery tube bent as shown in Fig. 269. The free end of the delivery tube dips into lime-water. The whole is maintained at a temperature of about 25° C. Fermentation soon becomes apparent and bubbles of gas passing through the lime-water turn it milky, showing that carbon dioxide is being evolved. When fermentation appears to have ceased the contents of the flask are

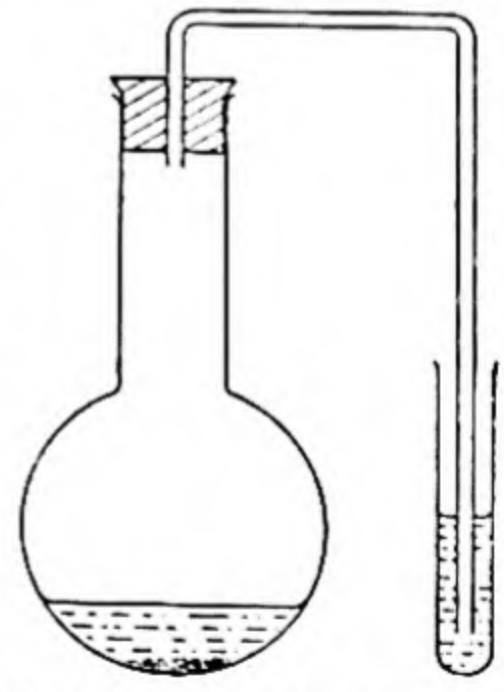


FIG. 269 – Apparatus for the preparation of Ethyl Alcohol.

fractionally distilled. In this way a solution of alcohol in water is obtained, containing a considerable proportion of alcohol. By repeated distillation, and final standing over metallic calcium, pure (absolute) alcohol may be obtained, though with the quantities suggested above the yield would be too small to make complete purification worth while.

CHAPTER 25

Elimination of Waste Matter

As a result of active metabolism a variety of waste products, other than carbon dioxide and water, must of necessity be formed. The problem of their elimination has therefore to be faced, and in this connexion animals and plants exhibit a fundamental discrepancy. Whereas in animals end-products of metabolic activity are expelled from the body at regular and frequent intervals, those of plants are normally withdrawn from circulation and deposited in an innocuous form in some part of the organism. Indeed they may actually fulfil some useful purpose even in this condition, as will be evident by a study of examples given later in this chapter, whilst many of them are of considerable commercial importance. A compound may be regarded as waste matter when it no longer plays any part in metabolism or provides an essential part of the structural material of the living organism. In accordance with their different fate, and to some extent with their chemical composition, the waste products of animals and plants will be dealt with separately.

Elimination of Waste

This may assume one of two well-defined forms.

(A) EXCRETION. By this is implied the elimination of the waste products of metabolism. This is to be sharply contrasted with secretion, a process concerned with the elaboration and liberation, by cells of the organism, of substances of value to it in the carrying out of vital processes. In this connexion it is to be noted that many of the waste substances of plants, dealt with later in the present chapter, are secretions rather than excretory products. But though some of them are of use to the plant in various ways, they no longer take any active part in metabolism, so that they may be considered for present purposes as waste matter, and in any case no clear line of demarcation can be drawn. This secondary utilisation of metabolic by-products does not prevent their being so regarded.

(B) DEFAECATION. This phenomenon is confined to animals and the insectivorous plants. It consists of the passage out of the body of those parts of the food which have never been rendered soluble and thus have never been absorbed into the body. Consequently they never form a part of the tissues of the body and hence can never play a part in metabolism. They remain fundamentally distinct from excretory products.

Thus the substances involved in defaecation are invariably solid, whereas excretory products may be gaseous (carbon dioxide produced

as a result of respiration – a fundamental part of metabolism), or they may consist of nitrogenous and other substances in solution. It is these latter substances which are for consideration here, and it will be well first to consider the organs responsible for the conversion of excretory products to their final stage of decomposition and their subsequent elimination.

Excretory Organs

In the Protozoa contractile vacuoles exist, and to these has previously been attributed the function of excretion. This is only party true. In members of this phylum most liquid waste matter probably escapes by diffusion through the surface. The main function of the contractile vacuole is to eliminate water which has entered the body, either as a result of the osmotic pressure of its protoplasm, or in its food vacuoles during feeding. That this is so is forcibly suggested by the absence of contractile vacuoles in many marine Protozoa, living in a medium whose own osmotic pressure is so much greater than that of fresh-water. In those marine forms which have contractile vacuoles the rate of contraction is much slower than it is in their fresh-water relatives, and the amount of water eliminated corresponds exactly to the amount taken in as food vacuoles. It is possible, however, that during the passage of water through the body to constitute the contractile vacuole a certain amount of soluble waste matter passes into solution, so that it is eventually eliminated from the contractile vacuole.

In the Coelenterata – e.g., *Hydra* and *Obelia* – the large surface-volume ratio means that most of the excretory products pass out by diffusion. Nevertheless crystals of urates have been demonstrated in some cells of the endoderm, and are probably cast out via the coelenteron. Further, a great majority of the Coelenterata have symbiotic Algae (page 669), which absorb much of their carbon dioxide and nitrogenous waste products.

In the Platyhelminthes, exemplified by *Taenia*, the excretory organs take the form of long, branching tubules, ramifying through a considerable part of the tissues of the animal. The finest branches terminate in flame-cells (page 40). The excretory products are eventually shed to the exterior by a pair of pores.

The Annelida are characterised by the possession of well-developed excretory organs, known as nephridia, the structure of which in *Lumbricus* has already been described (page 59). Each opens at one end into the coelom and at the other to the exterior. The dorsal pores of *Lumbricus* are probably of excretory function.

In the Arthropoda a certain diversity of structure of excretory organs is encountered. Thus the insects typically possess Malpighian tubules, which extend into the haemocoel and absorb from it waste substances. These are passed into the gut and discharged with the faeces. These

structures, like the excretory organs of Platyhelminthes and Annelida, are ectodermal in origin, being formed by a series of evaginations from the anterior end of the proctodaeum. In other Arthropoda – e.g., the Crayfish – the excretory organs are mesodermal, consisting of a pair of sacs, each enclosing a portion of the coelom, itself so severely restricted in the Arthropoda. Such mesodermal organs are known as coelomoducts.

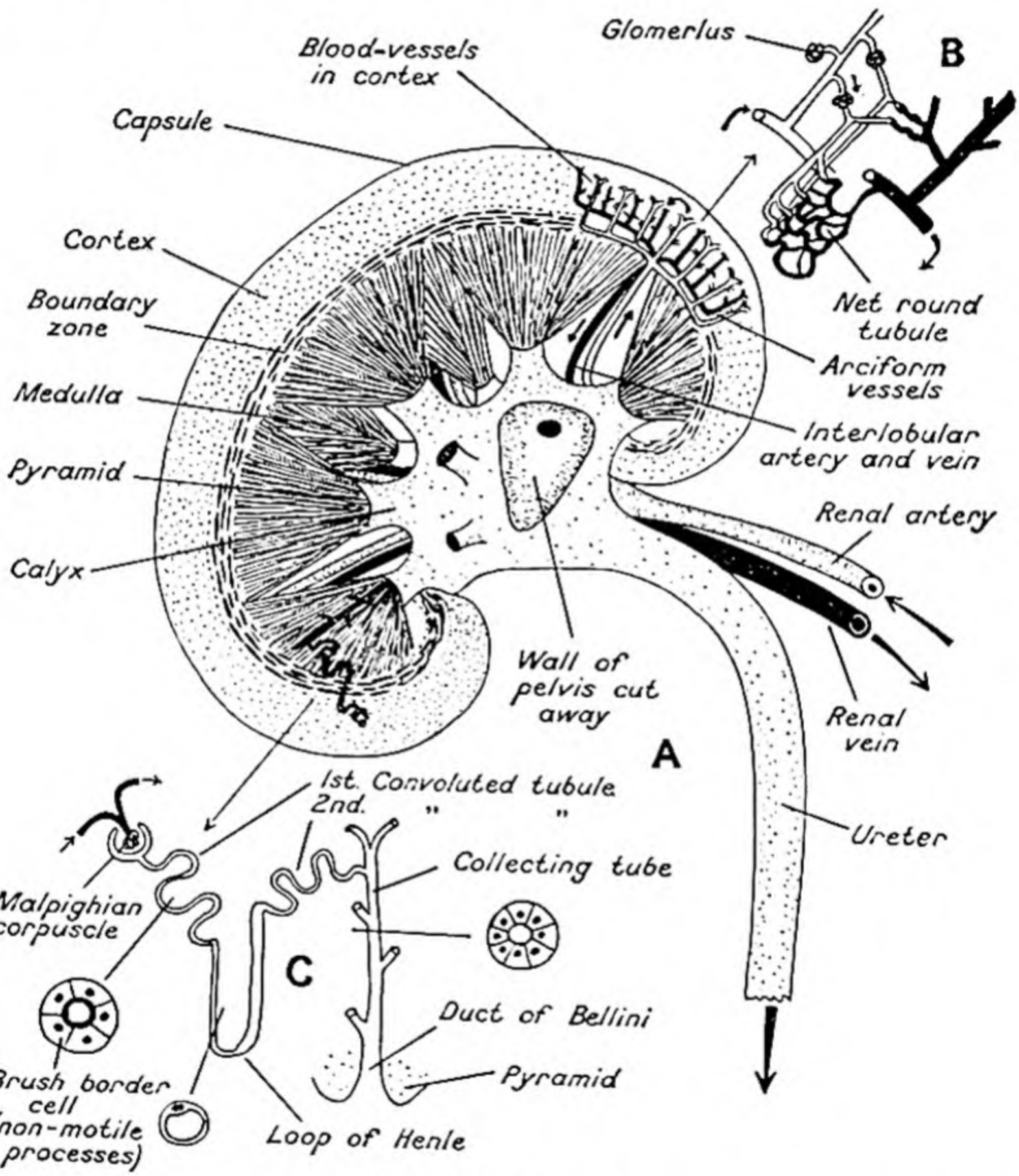


FIG. 270 – Kidney
A., Median half of a human kidney; *B.*, Blood-vessels associated with a tubule: *C.*, A single tubule.

In the Mollusca also the excretory organs are of mesodermal origin, consisting of a pair of tubes communicating between the pericardium and the exterior.

Branchiostoma, and allied forms, are remarkable amongst the Chordata in that their excretory organs are ectodermal nephridia. They possess flame-cells, and project for some distance down the primary gill-bars, collecting waste matter from the coelom in that region. Each opens into the atrium by a minute pore, just above a tongue-bar.

The remainder of the Chordata possess mesodermal kidneys, by means of which excretion is effected. Each consists essentially of a mass of much subdivided tubules, bearing cup-shaped evaginations, known as **Bowman's capsules**. Into the cavity of each Bowman's capsule extends a branch of the artery and vein supplying the kidneys, their capillaries

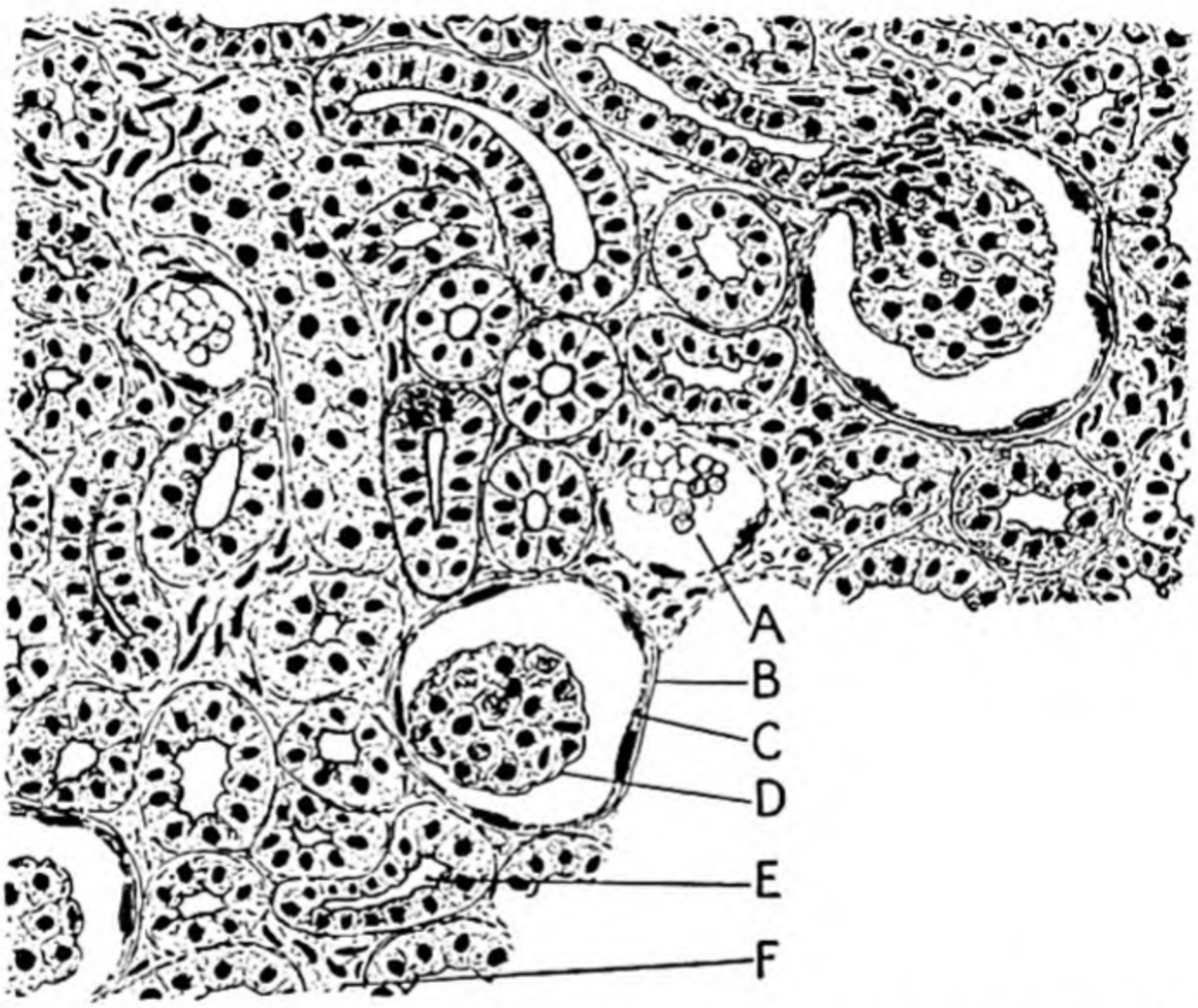


FIG. 271 – Portion of a longitudinal section through the kidney of Man.
A., Blood-vessel; *B.*, Basement membrane; *C.*, Endothelium of capsule; *D.*, Glomerulus, covered with reflected endothelium of capsule; *E.*, Uriniferous tubule; *F.*, Connective tissue.

ramifying to form a **glomerulus**. The composite structure, capsule and glomerulus together, is known, as a **Malpighian corpuscle**. During the passage of blood through the glomerulus, water, together with all molecules and ions in the blood plasma small enough to diffuse through the membrane, passes into the lumen of the capsule. Protein molecules are presumably too large to escape from the capillaries of a glomerulus. The waste products are then conveyed away in solution, and during their

passage through the remaining tubules of the kidney a certain amount of water, mineral salts and sugars is resorbed, whilst more nitrogenous products are actively excreted by the cells of the tubule. The mammals, and indeed most groups, thus excrete solutions of nitrogenous waste products, usually urea or ammonia, but it is interesting to note that insects, birds and reptiles conserve water by excreting solid uric acid. They thus resorb almost all the water as the excretory products pass down the Malpighian tubules or kidney tubules. This type of excretion is probably related to the long embryonic life in the egg, where the accumulation of soluble ammonia or urea would presumably prove toxic. Ammonia is the characteristic nitrogenous waste in aquatic animals. Having passed through the kidneys the urine is conveyed to the exterior along a pair of ducts, known in fish and Amphibia as Wolffian ducts, and in the remainder of the vertebrates as ureters (see page 613).

Chemistry of Excretion

In order to understand the chemistry of excretion it is essential to trace the fate of food materials from the time of absorption into the blood. The metabolism of these substances may therefore be considered under three heads, namely those of carbohydrates, fats and proteins. It should be realised that many of the reactions involved cannot be carried out in the laboratory, but are the sole province of living organisms.

(A) CARBOHYDRATES. Carbohydrates are absorbed as the monosaccharides, galactose most rapidly, then glucose, and finally fructose. Galactose and fructose become converted into glucose in the portal blood-stream, after which some of the glucose is converted into glycogen in the liver, whilst the remainder is retained in circulation as the carbohydrate currency. The concentration of sugar in the blood is kept constant, for if it rises above a certain definite maximum, known as the threshold value, the excess is excreted in the urine. In muscles, too, some of the glycogen is converted into glucose. In a working muscle a portion of this glucose is converted into lactic acid, about one-fifth of which is later oxidised to carbon dioxide and water, whilst the remainder is reconverted into glucogen, partly in the muscle itself and partly in the liver, whither it has been carried in the blood-stream. Some of the waste carbohydrate material may reach the urine either as lactic acid itself, or in the form of a lactate, the salt of the acid.

(B) FATS. After absorption the derivatives of the fats, namely, fatty acids and glycerol, are distributed in the lymphatic system, and to a lesser extent in the portal blood-system. In the comparative absence of fats from the diet these compounds may be formed from excess carbohydrate and even protein material. It is believed that most fatty acid metabolism occurs in the liver. In general it takes the form of the oxidation of the hydrogen attached to the β-carbon atom – i.e. the one neighbouring that directly connected with the COOH group. Thus, if butyric acid be taken

as a simple example, acetoacetic acid is formed, as shown in the equation:

$$\overset{\beta}{CH_3}\,\overset{\alpha}{CH_2}\,CH_2\,COOH + 2O = CH_3\,CO.\,CH_2\,COOH + H_2O$$

Butyric acid — *Acetoacetic acid*

This may then be further oxidised, with the formation of acetic acid, water and carbon dioxide.

$$CH_3\,CO.\,CH_2\,COOH + 4O = CH_3\,COOH + 2CO_2 + H_2O$$

Acetoacetic acid — *Acetic acid*

This is then finally completely oxidised to carbon dioxide and water.

$$CH_3\,COOH + 4O = 2CO_2 + 2H_2O$$

Acetic acid

Instead of behaving as shown above part of acetoacetic acid may

(i) Become reduced to β-hydroxybutyric acid:

$$CH_3\,CO.\,CH_2\,COOH + 2H = CH_3\,CH(OH)\,CH_2\,COOH$$

Acetoacetic acid — *β-hydroxybutyric acid*

or (ii) Become converted into acetone:

$$CH_3\,CO.\,CH_2\,COOH = (CH_3)_2\,C{=}O + CO_2$$

Acetoacetic acid — *Acetone*

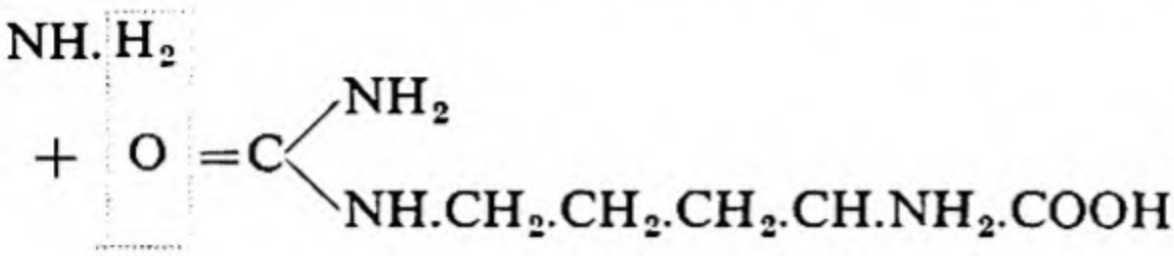
Thus, in such an example, the urine may contain small quantities of acetic acid, acetone and β-hydroxybutyric acid. But the presence of glucose appears to be essential for the normal metabolism of fatty acids, for in its shortage the amount of acetone and β-hydroxybutyric acid, and analogous products, may be increased to as much as three hundred times the normal content.

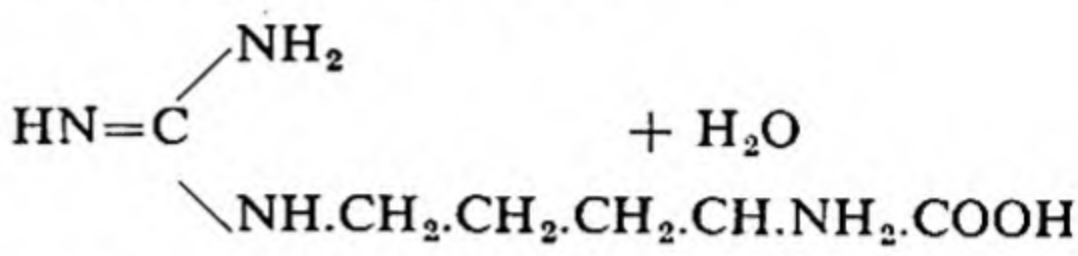
(C) PROTEINS. Proteins enter the blood as amino-acids, of which there is always a large excess. Unlike fats and carbohydrates, these acids cannot be stored by the animal, so the excess must be eliminated. Several hypotheses have been advanced in explanation of the formation of urea from amino-acids, and the following is the one for which most direct experimental evidence is claimed. According to this hypothesis, ammonia and carbon dioxide, under the influence of the amino-acid, *ornithine*, give rise to urea in the manner suggested in the equations below.

$$\begin{matrix} & NH_2\,H \\ & + \\ O = C = & O \\ & + \quad H \end{matrix} \quad -NH.CH_2.CH_2.CH_2.CH.NH_2.COOH =$$

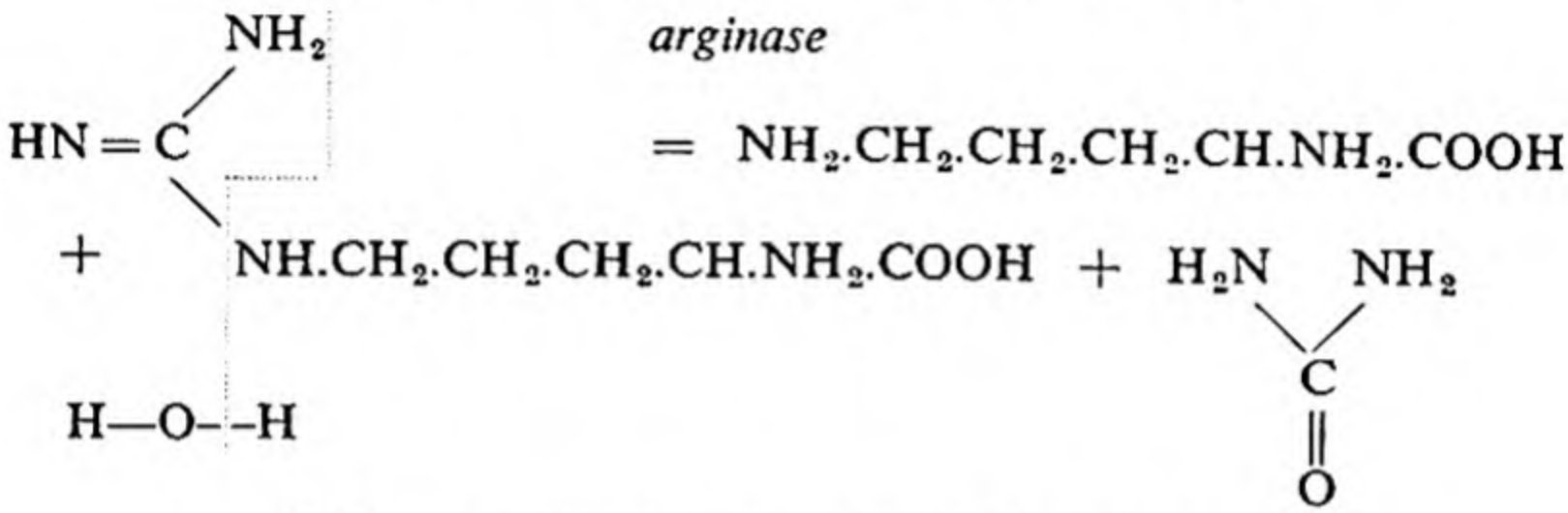
$$O{=}C\begin{matrix}\diagup\,NH_2 \\ \diagdown\,NH.CH_2.CH_2.CH_2.CH.NH_2.COOH\end{matrix} \quad +H_2O$$

$$NH_3 + CO_2 + \textit{ornithine} = \textit{citrulline} + H_2O$$





$$NH_3 + \textit{citrulline} = \textit{arginine} + H_2O$$



$$H_2O + \textit{arginine} = \textit{ornithine} + \textit{urea}$$

Krebs claims that this cycle has been shown to operate in mammals, fish, the frog and *Testudo*, but not in birds. Where it does occur, the ammonia is presumably formed by de-amination of amino-acids in the liver, as a result of which the nitrogen is removed as ammonia, leaving the free acid or its hydroxy-derivative. Thus deamination may occur as follows:

$$R.CH.NH_2.COOH + 2H = R.CH_2.COOH + NH_3$$

The ammonia has but a momentary free existence, after which it is presumably converted into urea in a manner at least analogous to that described above. It was formerly maintained that cyanic acid was formed as an intermediate product, afterwards being converted into ammonium cyanate as a result of its reaction with ammonia. Intra-molecular change resulted in the conversion of the ammonium cyanate into urea, a substance isomeric with it. But against this hypothesis, and in favour of the one outlined above, is the experimental fact that, whereas attempts to prepare urea by bringing solutions of ammonium cynate into contact with liver tissue have failed, positive results have been obtained by the use of a similar technique to demonstrate the formation of urea from ammonia and carbon dioxide, under the influence of the amino-acid, ornithine.

Osmo-regulation

Animals often exist in a medium whose osmotic pressure differs from that of their body fluids. For smooth and continuous metabolic function this difference has to be maintained, or, put another way, each animal has an optimum osmotic pressure for its body fluids, and this optimum ideally should be kept constant, regardless of disturbing external factors. It is the function of osmo-regulation to maintain this constancy. In the case of terrestrial animals this can be achieved only by the very careful regulation of water loss. Thus the skin as a whole acts as a relatively impenetrable barrier against uncontrolled loss of water. Within, it is the function of the kidney tubule to maintain this constant condition. Quite apart from maintaining a constant osmotic pressure of tissue fluids, even the viscosity of the blood must be preserved – i.e. the blood itself must not be allowed to circulate in a 'diluted' condition. So many functions of the blood depend upon this. Even the transport of oxygen, performed by the erythrocytes (page 327), could not be adequately achieved with 'diluted' blood. In aquatic animals the threats are –

(i) entry of water
(ii) loss of salts
} in fresh water

(iii) loss of water
(iv) entry of salts
} in sea water

The corresponding remedies are –

(i) impermeability
(ii) expulsion of excess water or salts
(iii) conservation of water or salts.

Throughout the whole vertebrate series the structure and function of the kidney have remained virtually unchanged. With special reference to the problem of osmo-regulation in fish, it will be instructive to analyse the methods by which this very important function of osmo-regulation is achieved. Fresh-water fish eliminate a very dilute urine by the almost total resorption of solutes from the glomerular filtrate. Sea-water fish excrete salt either through the kidneys or through the gills, where special secretory cells are often present. Cartilaginous marine fish, including *Scyliorhinus*, adopt the rather remarkable expedient of resorbing considerable quantities of urea from the glomerular filtrate and retaining this in the blood so as to achieve an osmotic pressure slightly above that of the sea water. Thus the eliminated urine is fairly dilute.

In general, marine animals which, like cartilaginous fish and most invertebrates, cannot adapt themselves to a fresh-water habitat, are described as *stenohaline*. Those whose osmo-regulatory mechanisms are more flexible are able, like the salmon, which is marine for part of its life and fresh-water for the remainder, and estuary-dwellers, to adapt themselves to either habitat. They are described as *euryhaline*. The

enormity of the problem of osmo-regulation by aquatic animals is to some extent reduced for most of them by the relative impermeability of their outer covering.

Waste Matter in Plants

The organic waste products of plants are classified according to their chemical composition, and a number of such classes will be treated individually.

(A) RESINS. Resins are aromatic compounds consisting of carbon, hydrogen and oxygen, and are acidic in nature. This latter property imparts to them a pungent taste, as a result of which they may be distasteful to herbivorous animals. Being antiseptic they are further significant in the temporary closure of wounds. Some are hard in nature, whilst others – the balsams – have a lower melting-point. Many of them are themselves of considerable technical importance, whilst others are used in the manufacture of varnishes and gums.

(B) TANNINS. The tannins comprise a class of chemical substances characterised by response to certain reagents, though somewhat diverse in structure. Thus they will reduce Fehling's solution and are turned brilliant red by ammonia. They all have an astringent taste, on account of which they may function for protection against herbivorous animals. Tannins occur commonly in the bark of many trees and are used for the conversion of hide into leather, which they do largely as a result of bringing about the coagulation of the protein substances of the skin. With ferric salts they are much used in the manufacture of ink.

(C) ALKALOIDS. These are basic organic substances always containing nitrogen. In the plant, they frequently occur in combination with organic acids. Their poisonous nature may well render them protective in function. They are of considerable commercial importance, and amongst them may be noted cocaine, hyoscine, morphine, nicotine, quinine and strychnine, all of which are extracted from plants.

(D) GLUCOSIDES. Not all glucosides are waste products. Some function as storage substances – e.g. amygdalin of the bitter almond. But a number of them constitute the characteristic pigments of many flowers. Thus **anthocyanins** are mainly responsible for red and blue colours and **flavones** for cream colour. (Yellow and orange colours, on the other hand, often owe their existence to carotene, a constituent of chlorophyll. This pigment is an unsaturated hydrocarbon, and not a glucoside.) The mustard-oil obtained from many Cruciferae (page 631) is a product of hydrolysis of a glucoside. Some plant pigments are employed as a source of dyes.

The appearance of characteristic pigments in the leaves of deciduous trees in the autumn affords a means of removal of certain waste products at leaf-fall.

It must not be imagined, however, that autumn coloration is entirely

associated with the excretory process, and it will be convenient at this point to examine the sequence of events in, and the purpose served by, this most attractive seasonal phenomenon. Primarily the processes leading to the development of autumnal coloration are specifically concerned with the withdrawal of materials likely to be of service in a subsequent period of growth. In the early stages it will be noticed that, in general, red is the predominant colour. This is due to the formation of anthocyanins in the cell-sap, a synthesis of which many plant-tissues are capable, but only in certain physiological conditions. Amongst these the most significant is a high sugar concentration, and this is precisely satisfied at this season, for starch is now being hydrolysed to facilitate translocation to permanent organs for winter storage. Eventually all reserves of carbohydrate material are thus removed and the red colours give way to yellows. This is due to the mobilisation and removal of the green components of the chlorophyll complex, leaving the carotene and carotenoids to display their presence. In the final stages even these are withdrawn and, with the gradual death of the leaves, the sombre brown is all that remains to remind us of the verdant splendour of life, now rapidly passing.

These changes vary not only with the types of tree but also with environmental conditions. The leaves of some trees never redden, and examples of these are afforded by the beech and native English oaks. A clear, bright autumn, generally accompanied by night frosts, will be productive of much more brilliant colours, especially red, than will a damp, foggy one. This is explained on the grounds that at low temperatures there is a much more rapid conversion of starch into sugar, so that in these conditions anthocyanins are readily formed, especially since the rate of evacuation of sugar from the leaves is retarded by precisely the same low temperature as encouraged its formation.

In broad principles it has been established that the sequence of events in the ripening of fruits follows much the same course as that shown in the development of autumn colours in leaves, and both may be regarded as manifestations of senescence, which in plants, unlike animals, is a phenomenon often repeated in the lifetime of the individual.

(E) ETHEREAL AND ESSENTIAL OILS. The ethereal oils responsible for the characteristic odour of many flowers or leaves of plants consist of a mixture of various hydrocarbons, known as **terpenes**, and their oxygen derivatives. Examples are afforded by lavender, mint, clove and *Eucalyptus*. Their commercial importance lies in the manufacture of perfumes and antiseptic oils – e.g. *Eucalyptus* and menthol (from the pepper-mint). The so-called essential oils, of function similar to the ethereal oils, are esters of some of the higher acids.

(F) CALCIUM OXALATE. Calcium oxalate is one of the most widely distributed of plant waste products. It may occur in the form of single crystals, each occupying the greater part of a cell, or of bundles of smaller

crystals, radiating from a common centre or lying parallel to each other, in which cases they are known as **raphides**. Calcium oxalate most frequently makes its appearance in cells where active metabolism has been proceeding for some time, and very important is its formation in the leaves of deciduous trees just prior to leaf-fall. The significance of this lies in the fact that this waste product is then eliminated when the leaves are shed.

A study of the foregoing examples will serve to show how the plant withdraws from circulation substances which are no longer capable of taking any active part in metabolism – i.e. waste matter. Only in the case of deposition in leaves and flowers are such substances entirely eliminated from the plant. Often they are employed by the plant to fulfil quite important functions, as is exemplified by the colours of flowers for the attraction of insects which effect pollination, and by the protective nature

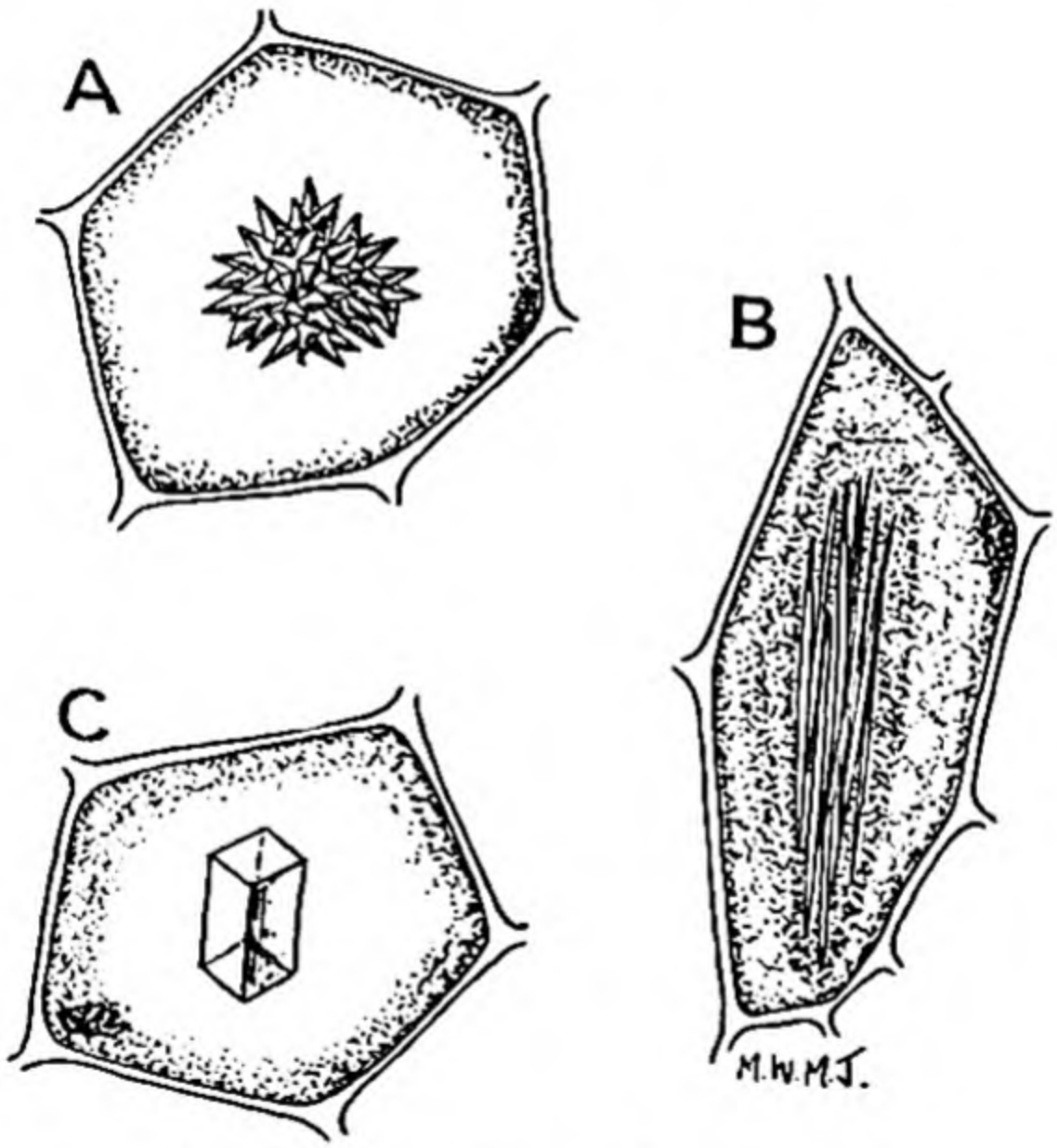


FIG. 272 – Raphides within plant cells.
A., A stellate cluster; *B.*, Parallel crystals; *C.*, A single, large crystal.

of the resins, tannins and alkaloids. But in general there is to be noted here a marked discrepancy between plants and animals, for the latter do not merely withdraw metabolic by-products from circulation, but totally eliminate them from their bodies at frequent and regular intervals. It must,

of course, be remembered that oxygen (from photosynthesis) and carbon dioxide (from respiration) are metabolic by-products of plants.

PRACTICAL WORK

Examine a prepared section of the kidney of the frog or rabbit, looking carefully for Malpighian corpuscles. Draw.

Extract urea from a sample of urine, according to the instructions given in practical text-books of Organic Chemistry.

Cut sections of leaves of deciduous trees in the autumn. Examine for raphides.

CHAPTER 26

Irritability and Movement

Irritability

Irritability – the ability to receive stimuli and transmit impulses from the environment – is a fundamental property of protoplasm. Such a property can be detected in a living organism only as the response to various stimuli is observed. Such response almost invariably results in some form of movement, so that the two correlated phenomena of irritability and movement may best be considered conjointly. That protoplasm is able to respond to stimuli without the development within the organism of special receptor mechanisms is clearly indicated if the behaviour of *Amoeba* and *Paramecium* is studied. During the extension of a pseudopodium by *Amoeba* it is possible that contact may be made with a particle of food material. In this case, as already described (page 6), the particle is ingested. But if the food particle be replaced by a foreign body, such as a grain of sand, the pseudopodium is withdrawn and a new one is extended in a fresh direction. This leads to the conclusion that *Amoeba* exhibits a differential irritability, by which it is implied that not only has the organism the power to respond to stimuli, but also that different stimuli elicit different responses. The fact that after the withdrawal of a pseudopodium from a grain of sand a new one is extended indicates a certain power of conduction of impulses through the general protoplasm of *Amoeba*.

Behaviour of Paramecium

The response of *Paramecium* to various stimuli has been worked out in considerable detail. When this organism comes into contact with a foreign body it is found momentarily to move in the reverse direction. This movement is effected by a reversal of the cilia beat. Immediately afterwards the organism becomes slightly rotated about its centre and then moves forward in the changed direction. This change of direction is brought about by the differential rate of the beating of the cilia on the two sides of the animal. The whole sequence of movements described above is known as a **phobotaxis**, or 'avoiding reaction', though, as will be seen later, it is only imperfectly adapted to the protection of the organism from injurious substances. Let it be imagined that a drop of very dilute ($\frac{1}{2}\%$) salt solution be introduced with a very fine pipette into a drop of *Paramecium* culture on a microscope slide. This drop of salt solution remains empty of paramecia, for they perform the avoiding

reaction on coming into contact with its surface. But if this salt solution be replaced by acetic acid (about 0.02%), the paramecia are found to pass into the drop of acid and are unable to escape from it. This is because they fail to perform the avoiding reaction on reaching the surface of the acid, but they do perform it when, once within the acid, they attempt to regain the water. *Paramecium* reacts equally readily to temperature-change. If one end of a shallow glass trough containing *Paramecium* culture be heated at 40° C. and the other maintained at 25° C. the organisms are found to collect at the cooler end. On the other hand, if the temperature at the end at 40° C. is reduced to 10° C., they continue to collect at the end at 25° C. This would appear to be their optimum temperature, and they are prevented from leaving it by the performance of the avoiding reaction when tending to move towards a markedly warmer or cooler region. In a precisely similar manner *Paramecium* is enabled to select a moderately illuminated region of its environment in preference to total darkness or an intense light. A somewhat artificial instance of response by *Paramecium* to a stimulus may be demonstrated by passing a minute electric current through a culture. The organisms are found to move in the direction of the positive ions, as may be verified by a reversal of the direction of the current.

Taxes and Tropisms

Phototaxis is a phenomenon similar to those described for *Paramecium* and is encountered in many non-cellular Algae, as well as in the swarm spores of the filamentous Algae. These bodies possess locomotory powers on account of the presence of flagella, and the direction of their movement is controlled principally by the angle at which incident light is reaching them. Their normal response is to move in the direction of light, providing that the latter is not too intense. The influence exerted on these plant organisms by the direction and intensity of light is known as phototaxis, and shows obvious resemblances to the response by *Paramecium* to various external conditions.

Chemotaxis is the term applied to the response elicited from some motile plant elements by the presence of specific chemical substances. It is commonly found exhibited by the male reproductive bodies of Algae, mosses and ferns, for example. Here the spermatozoids are attracted towards the eggs as a result of positive chemotaxis. In the case of ferns the neck of the archegonium (page 227) produces malic acid, whilst in mosses the attraction is effected by means of cane-sugar solution. Many Bacteria are positively chemotactic to particular organic or inorganic substances, so that here the response is connected with nutrition, whereas in the forms mentioned above it is of reproductive significance.

Such movements as those described above, occurring in direct consequence of particular stimuli, are known as **taxes**. Whilst the vast majority of plants are incapable of movement as a whole, certain parts

of them are able to move to some extent. But certain stimuli exert a marked directional influence on the direction of elongation and orientation of parts of attached plants, and the responses elicited by these stimuli are known as **tropisms.** They correspond to the taxes of motile plants or plant-products, such as spermatozoids.Thus, in response to very definite stimuli, the direction of elongation of the growing tips of the root and shoot may be modified, whilst the plane of the lamina of a leaf may be rotated. The experimental evidence for the existence of tropisms will be considered in the present chapter, whilst in Chapter 27 an attempt will be made to give some indication of the way in which stimulus and response are related. Depending on whether the stimulus is due to light, gravity or water, the responses are described as **phototropism, geotropism** and **hydrotropism** respectively. They will now be considered individually.

Geotropism

Curvature occurs only if the gravitational force is not acting equally on all sides of the growing root or shoot, and stops again when equilibrium is restored. This is evident if a seedling is placed in such a position that the radicle lies in a horizontal plane. Curvature then proceeds until the radicle becomes vertical, when the gravitational force is distributed equally about all points. Such geotropic curvature is due to more than the mere weight of the radicle. That this is so is evident from the fact that shoots grow vertically upwards in defiance of gravity. It may also be forcibly demonstrated for radicles themselves. Thus, two lots of germinating seedlings are taken, and the one lot killed by boiling. All are then fixed on to corks and attached to a containing vessel in such a way that their radicles lie horizontally on the surface of some mercury. The mercury is covered with a thin layer of water to prevent the drying up of the radicles. The radicles of the dead seedlings remain in this position, whilst the others penetrate the mercury for some distance, and thus must be capable of overcoming considerable resistance.

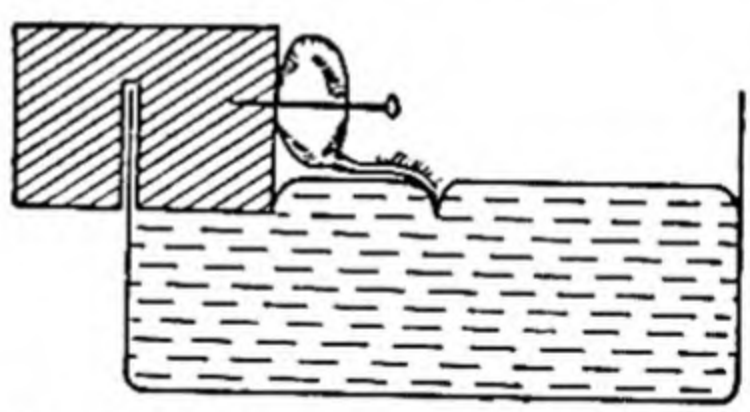


FIG. 273 – Apparatus for the demonstration of active geotropism of the radicle of a germinating seed. For description see text.

The effect of the elimination of gravitational response may be observed with the aid of a **klinostat.** This consists essentially of a revolving drum to which growing seedlings may be attached. If the drum be made to revolve in a vertical plane and seedlings are placed in such a position that their roots extend horizontally from it they will continue to grow in this direction as long as the revolution of the drum is maintained, since all parts of the growing radicles will be subjected in turn to the unequal stimulus. A control experiment is performed by placing seedlings in a

similar position on a stationary drum, when the normal downward curvature is observed.

In general, experiments on the nature and mechanism of geotropism are performed in darkness, thereby eliminating any contrary effects of light.

The geotropic response of various plant organs is interesting and

FIG. 274 – An electric klinostat, drawn from a photograph in a catalogue of Messrs. Flatters & Garnett Ltd. (By kind permission of the manufacturers.)

important. On the whole primary roots grow towards the source of stimulation, and are said to be positively geotropic, whilst primary shoots, described as negatively geotropic, grow away from it. Secondary roots are roughly diageotropic (see below), whilst tertiary roots are neutral in their gravitational response. Thus rhizomes and many creeping shoots establish the necessary equilibrium when growing in a horizontal position, and are said to be **diageotropic**. Some even may change their response at different periods of the life-history of the plant of which they form part. Thus in the poppy the flower stalks are at first positively geotropic, then, as the flower opens, they become diageotropic, and finally they exhibit a negative geotropism. Thus the bud of the flower is pendant, the open flower almost horizontal, whilst the capsule with its contained seeds is borne erect.

Experimental work has indicated that the regions of perception of the stimulus and of subsequent curvature are not identical. Thus, if the tips of growing radicles are removed and the radicles then placed in a horizontal position there is little or no curvature unless or until new tips

are formed. This indicates that the region of gravi-perception is the root tip. If, prior to this being placed in a horizontal plane, equidistant ink marks are made on the radicles it is observed that the region of curvature corresponds to the region of maximum elongation (page 419). Similar results may be obtained with shoots or leaves, and in this connexion the coleoptiles of grasses are particularly useful. The *coleoptile* is the hollow cylinder in which develops the first leaf. It is to be noticed in this case that curvature occurs at an appreciable distance behind the tip.

FIG. 275 – Germinating bean, prepared to show that the region of curvature of the radicle coincides with that of maximum elongation.

Phototropism

For experimental work a dark chamber is necessary. This consists of a wooden box, blackened on the inside to prevent reflexion. At one end is an adjustable slit for the admission of light, whilst at the other is a hinged door serving for the introduction into the chamber of experimental material. In general, it is observed that the shoot of a plant grows towards the source of illumination. If, however, the plant be rotated in a horizontal plane elongation continues to be vertical, for although illumination is still unilateral, each side of the plant in turn is exposed to the light. In almost all instances it is the conjoint effect of light and gravity which must be observed, owing to the difficulty of eliminating the latter and at the same time regulating the supply of light to the required condition. But if the geotropic effect is previously determined, then any departure from this behaviour in light must be due to phototropism. The net result of the two tropisms is not always the same, even for the same organs of different plants. Thus, if a pea seedling be grown in the dark chamber the plumule assumes an almost horizontal position, whilst the bean does not depart so far from the vertical. Presumably the negative geotropism is more forcibly expressed in the bean than in the pea. But it will be apparent that in both cases the positive response to light supersedes the negative response to gravity, otherwise the plumule would continue to grow vertically upwards.

Some roots are negatively phototropic, whilst the vast majority of shoots are positively so. Other roots appear not to respond to the presence of light. Leaves are principally **diaphototropic** – i.e. their laminae take up a position at right angles to the incident rays. Some leaves, however, notably those growing on plants subject to intense illumination, lie parallel to the rays. Only young leaves can modify their position in response to light, for, when the petiole has completed its growth, further curvature is not possible. The final position of the leaf is normally that at which it receives most light during each daily period of illumination.

Just as with geotropism so variations in phototropic responses in

certain plant organs may be observed. The flower-stalks of the ivy-leaved toadflax, for example, are positively phototropic until the fruits are ripening, when they become negatively so. Thus the seeds are dispersed in such a way that their chances of lodging in a crevice of the wall on which the plant is climbing are appreciably increased.

That the stimulus eliciting phototropic curvature is received at the tip of the shoot may be demonstrated by covering the terminal regions of some of a number of coleoptiles before exposing them to unilateral illumination, when it is observed that these depart but slightly from the vertical position. Again, as in the case of geotropism, the region of curvature is also the region of maximum elongation, as may be shown experimentally by the method employed to demonstrate the site of geotropic curvature.

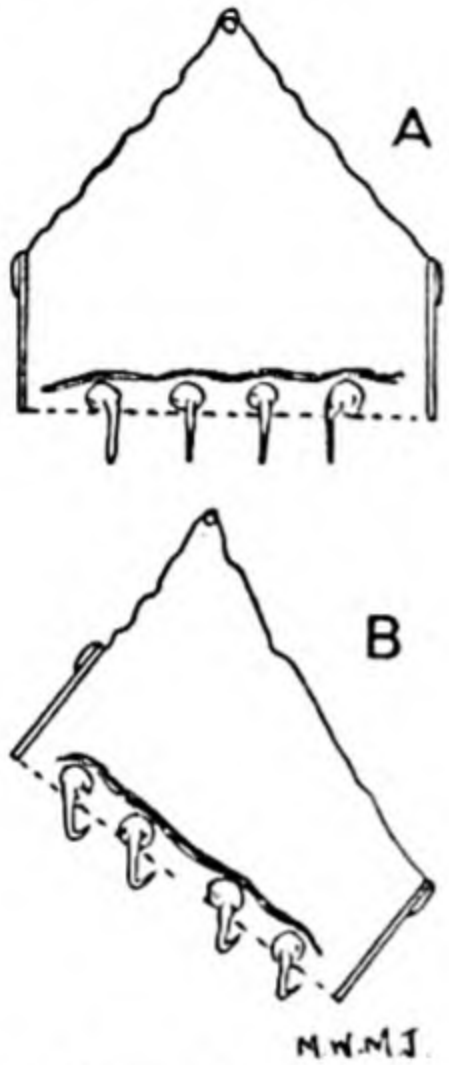


FIG. 276 – Apparatus to show the relative effects of water and gravity upon the direction of elongation of radicles. *A.*, When the sieve lies horizontally the radicles continue to grow vertically downwards. *B.*, When the sieve is tilted the proximity of water to one side of each radicle causes the curvature shown.

Hydrotropism

Roots respond very strongly to an uneven distribution of water, tending to move towards the nearest available supply. They are said to be positively hydrotropic. This is, of all, the most powerful directive influence on the growth of a root, as may be shown in the following experiment. Pea seeds are sown in moist sawdust contained in a wire gauze bent to a steep angle and fixed in the top of a beaker. Presently the radicles emerge through the interstices of the gauze, but soon afterwards bend towards the nearest supply of moist sawdust, which they re-enter. If the seeds are sown on a flat gauze and their radicles grow vertically downwards they are unable to regain the sawdust, since the water attracts each radicle equally all round, so that curvature cannot occur. It is to prevent this possibility that the gauze is sloped at as steep an angle as practicable. The natural significance of hydrotopism is that it ensures, as far as possible, that the roots of plants living in dry surroundings will reach any available moisture in the soil.

Conjointly these three tropisms largely regulate the form of plants, and particularly the relative positions of the various organs. Geotropism is primarily responsible for the downward growth of a root and the

upward growth of the stem, and especially is it important in seeds germinating within the soil, for the negative geotropic response of the shoot enables it quickly to reach the surface, whilst the positively geotropic root is soon growing vertically downwards. Hydrotropism exerts a further directive influence over the growth of a root, whilst phototropism is afforded but little opportunity of controlling the direction of elongation of the shoot, since continuous unilateral illumination is rarely encountered. It is important, however, in regulating the positions of leaves, and often the direction of growth of stalks bearing flowers and subsequently fruits. The attempted explanation of these complex phenomena in terms of hormones will be retained until the following chapter.

Conduction of Impulses in Animals

Whilst reception of stimuli and conduction of impulses appears to be a fundamental property of protoplasm, in the vast majority of animals it has become the specialised function of nervous tissue. In more primitive forms – e.g. the Coelenterata – there seems to be little or no control over the direction in which a given impulse may pass, for the nervous system assumes the form of a network. In higher animals an important function is the correlation of nervous messages, and this becomes progressively more significant as sense organs attain greater development, for in this way the animal is enabled to perceive a far larger number of stimuli. Nervous integration has become most highly developed in the Chordata,

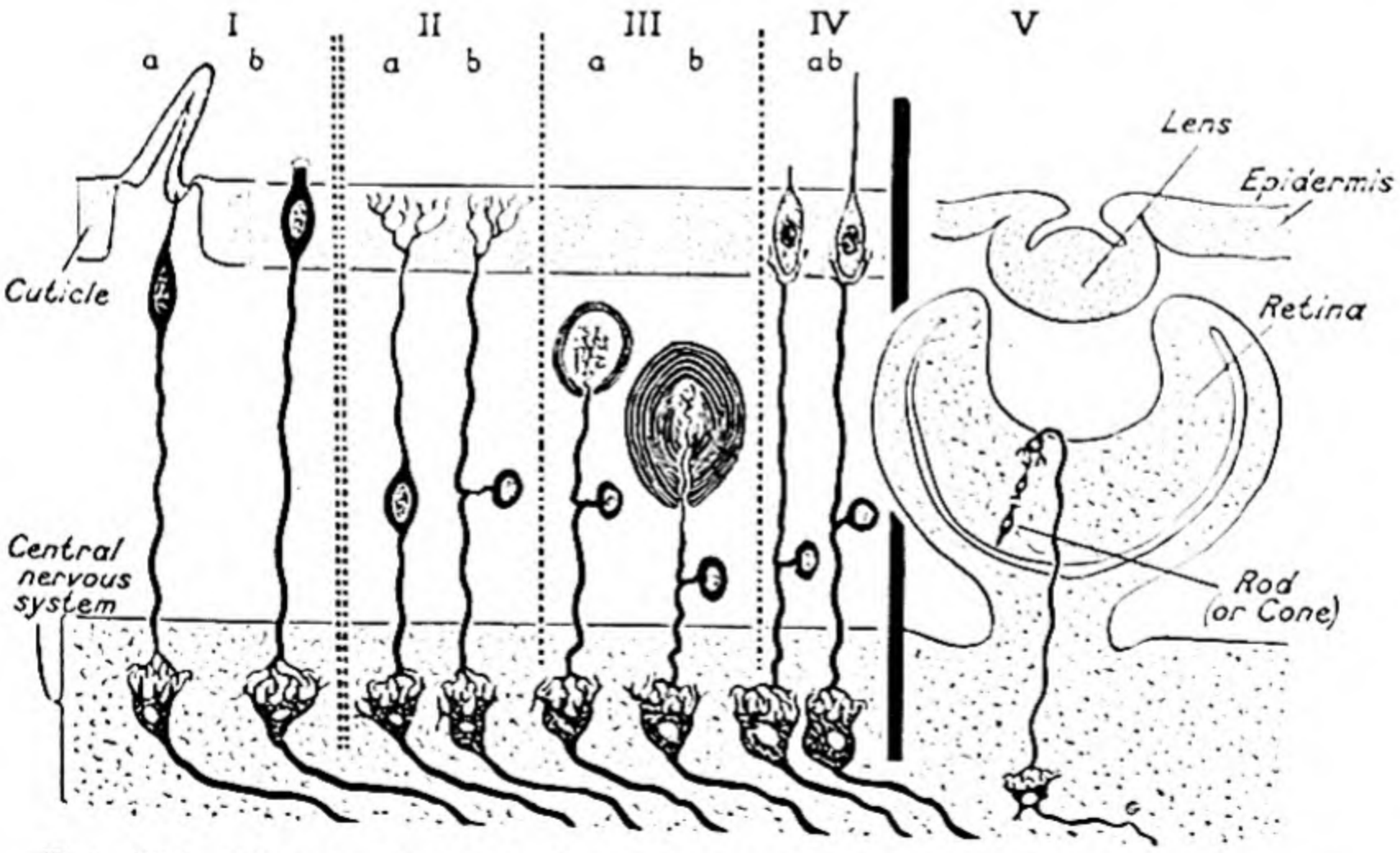


FIG. 277 – Diagram to show the main types of sensory mechanism in multicellular animals. For explanation see text.

and thus it will be best to consider the problem in this phylum.

Before proceeding to this, however, it is necessary to understand something of the sensory mechanism in multi-cellular animals in general. This is best achieved by a careful study of Fig. 277, using the text immediately following as a commentary.

I. *a*. Conduction usual in invertebates, where the sensory cell (in this case associated with an exoskeletal process) also produces the nerve fibre connecting it with the central nervous system.

b. Olfactory sense cell of a vertebrate, where this primitive condition still persists.

II, III and IV. In all cases the cell-body has retreated from the surface and is usually found in a dorsal root ganglion (in vertebrates).

II. *a*. Bipolar condition, as seen in fish and the embryonic stages of mammals.

b. Unipolar condition.

In both cases the distal fibre terminates in *free nerve-endings* in the surface layer. Many nerves to the viscera have similar, unspecialised endings.

III. *Tactile End Organs*. Here the distal end of the nerve is enclosed in a capsule of fibrous connective tissue.

a. The capsule is thin and the nerve-endings respond to weak

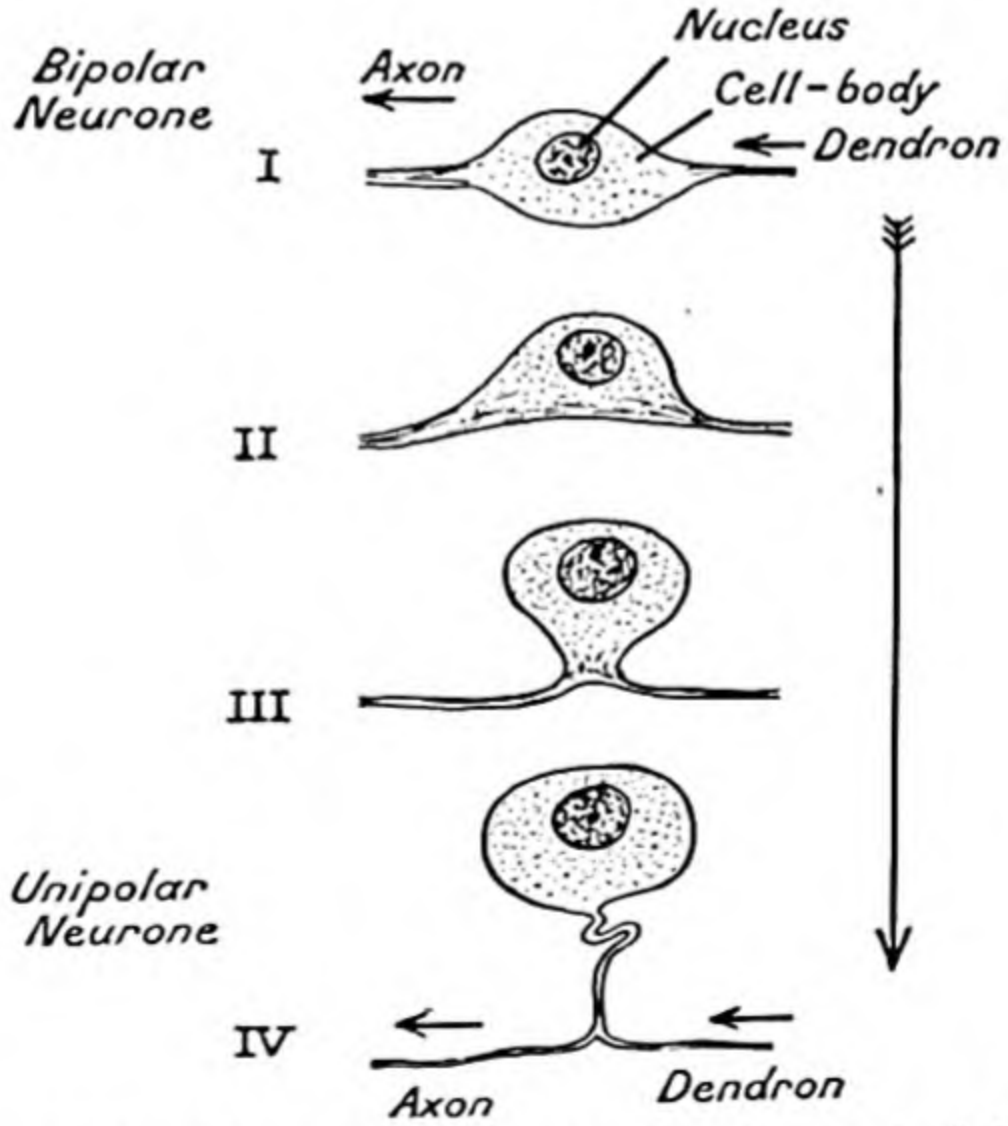


FIG. 278 – Diagram to show the development of the unipolar neurone from the bipolar condition seen in the embryo. In lower vertebrates (e.g. fish) the neurones remain bipolar.

stimulation – e.g. Meissner's corpuscles in the superficial layers of the dermis.

b. The capsule is thick and lamellated, whilst the organ is more deeply embedded and responds only to a higher level of tactile stimulation – e.g. Pacinian corpuscles.

Similar tactile receptors are found in the deeper parts of the body – e.g. tendons and ligaments – where they form part of the proprioceptive nervous system (page 465).

IV. Here the nerve endings receive their stimuli from specialised sensory cells. This is the common condition in vertebrate sense organs.

a. Sensory cell with short distal process – e.g. taste bud cell and neuromasts of lateral line in fish.

b. Sensory cells with long distal processes – e.g. cells of the cristae in the ampullae of the semicircular canals of the ear.

V. The special condition seen in the vertebrate eye. The retina of the eye is essentially an extension of the embryonic brain towards the surface, where its neurones can be directly stimulated by light. The lens, produced by the epidermis, provides a passive contribution to the efficiency of the retina. The sensory neurones (rods and cones) of the retina lie in the deeper layers (inverted condition). Each impulse passes through a double relay system before being conducted to the optic centres of the brain.

It should be remembered that not only are most sensory neurones epidermal in origin, but so also is the neural tube (brain and spinal cord) itself. The special condition in the retina is, therefore, not such an exception as at first appears.

Reflex Arc and Reflex Action

Although the majority of actions performed by any member of the Chordata are comparatively complex, it is found possible to resolve them into simpler components. In order to appreciate how this has been achieved it is necessary to study in detail the structure of the spinal cord. For this purpose it will be imagined that a transverse section has been cut in the region where a spinal nerve may be seen to enter. It must be clearly realised at the outset that a single nerve, as seen in dissection, is really a bundle of some hundreds of axons (page 336), all enclosed in a common sheath. For the sake of simplicity only two of these axons will be considered. Let it be imagined that the skin of the hand is irritated. This means that the skin of that region receives a stimulus, and it is therefore described as a **receptor organ**. The impulse so set up passes up the arm via a dendron into the spinal cord, penetrating the dorsal horn of its grey matter (Fig. 279). In view of its position it is called a **dorsal root**. Its cell-body occurs just outside the spinal cord, so that this particular nerve-cell has a dendron extending from the hand to the cell-body, and an axon from the cell-body to the grey matter of the spinal cord. Consequently it is described as bi-polar. Since this neurone carries

impulses from the receptor organ into the grey matter of the spinal cord it is described as **afferent**, or, alternatively, it is said to be a **sensory** nerve-fibre. Once within the grey matter the axon becomes subdivided to form a terminal arborisation. The branches thus produced establish near-contact with the dendrites of several cell-bodies but, again for the sake of simplicity, only one such will be considered at this point.

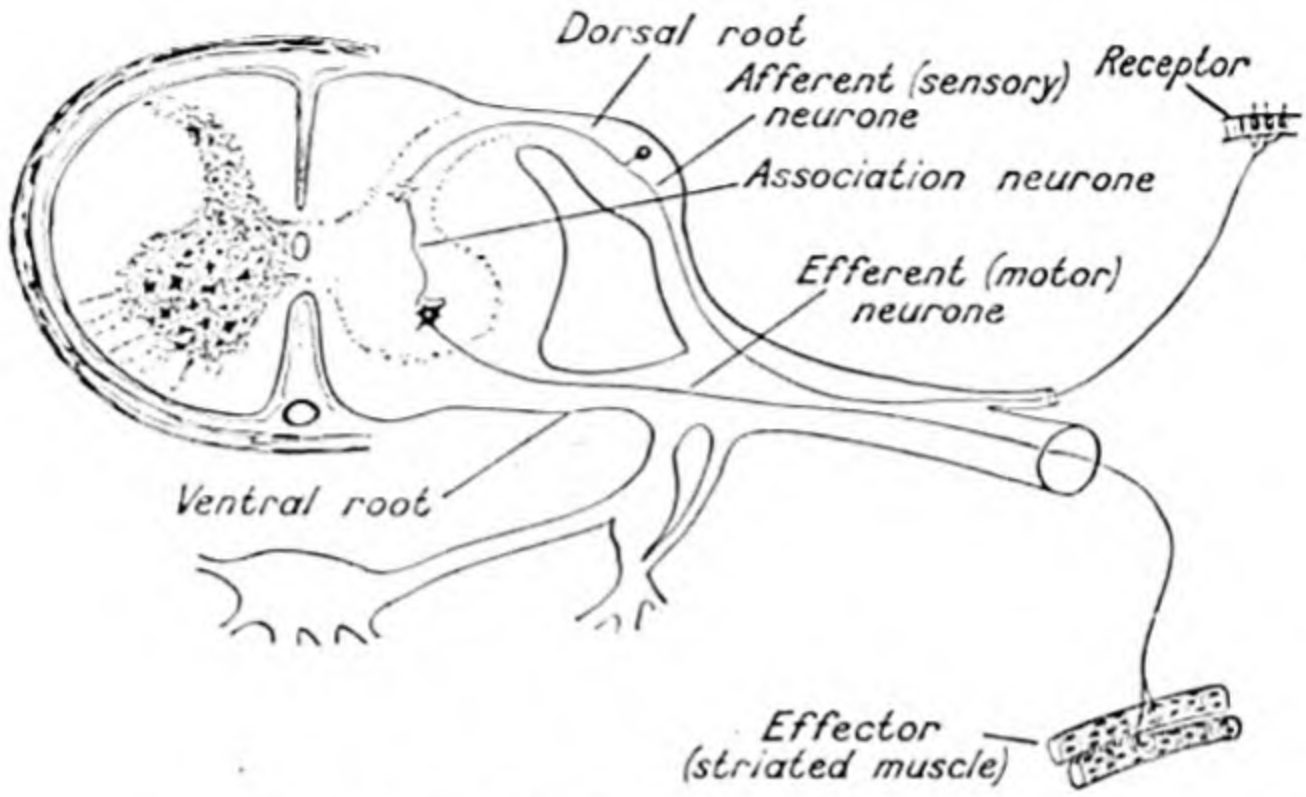


FIG. 279 – Simple somatic reflex arc.

In reality there is a minute gap, termed a **synapse**, between the nerve-fibres involved, across which the impulse is transmitted by diffusion of specific chemical substances. The cell-body concerned bears an axon which conveys the impulse to the ventral side of the spinal cord. The whole cell is termed an **association neurone** and in turn communicates with a further neurone, the axon of which leaves the ventral horn of the grey matter to run in the main arm nerve until such time as it emerges to penetrate some muscle of the arm (possibly the biceps), which is stimulated to contract, thus withdrawing the hand from the source of irritation. The muscle is therefore called an **effector** organ, whilst the neurone conveying the impulse to it from the spinal cord is described as **efferent**, or **motor**. The above is the simplest type of nervous path which can be depicted, and is known as a **reflex arc** (see Fig. 279), whilst the action which it accommodates is called a **reflex action**. It takes place without reference to the conscious brain, and impulses pass out of the spinal cord at the same level as that at which they enter – i.e. their only motion in the spinal cord is from its dorsal to its ventral surface through the grey matter: they are not transferred in an anterior or posterior direction. This simple nervous circuit is often described as the unit of nervous integration, and actions in general may be accounted for by a modified form of this simple mechanism. Since a spinal nerve consists of hundreds of such dendrons, the cell-bodies of the dorsal roots, since they all occur in

the same position, are visible externally as a swelling on the nerve. This is known as the **dorsal root ganglion.**

Association Neurones

Now let it be imagined that a stimulus be applied to the upper part of the hind leg of an animal, such that the fore-limb must be brought into action to remove the source of irritation. The receptor organ is provided by the skin of the leg, and from it a sensory fibre conveys the impulse to the grey matter at the base of the spinal cord. Here the terminal arborisation forms a synapse with the dendrites of an association neurone. The axon of the latter cell enters the white matter of the spinal cord and in it runs to the level of the fore-limb. Here it plunges again into the grey

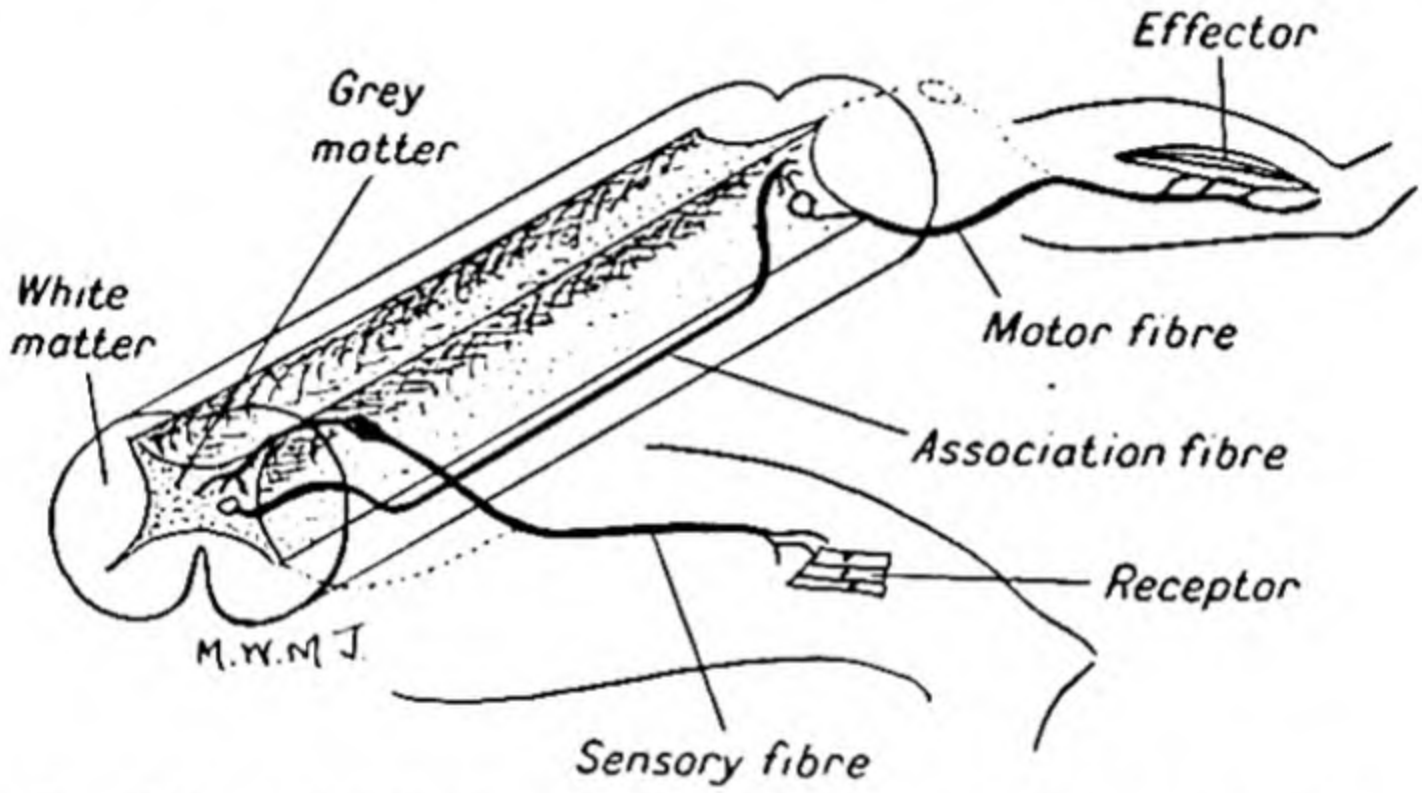


FIG. 280 – Diagram to illustrate the importance of an association neurone in the conduction of a simple impulse.

matter and breaks up to form a terminal arborisation. This forms a synapse with the dendrites of a true motor fibre, whose axon emerges from the ventral horn of the grey matter to pass to the muscles of the fore-limb.

White and Grey Matter

It will have been observed that a dorsal root always enters the grey matter by the dorsal horn, whilst a ventral root emerges from the same region of the spinal cord via the ventral horn. Thus the grey matter consists of the terminal arborisations of sensory fibres, the cell-bodies and dendrites of the motor fibres, and the association neurones connecting them. When an impulse is to be conveyed up or down the spinal cord or from one side to the other this is effected by an association neurone, whose axon travels in the white matter. Thus the white matter is composed of the axons of association neurones. In transverse section, there-

fore, the grey matter consists of a mass of closely packed nervous tissue, whereas in the white matter may be seen merely the cut edges of the axons.

Before proceeding further with the subject of nervous integration it will be wise for us to realise that the endeavour to analyse the function of the nervous system has resulted in an exaggerated simplification of an extremely complex mechanism. Thus the reflex arc in its classical conception probably never functions as such. A simple stimulus may be

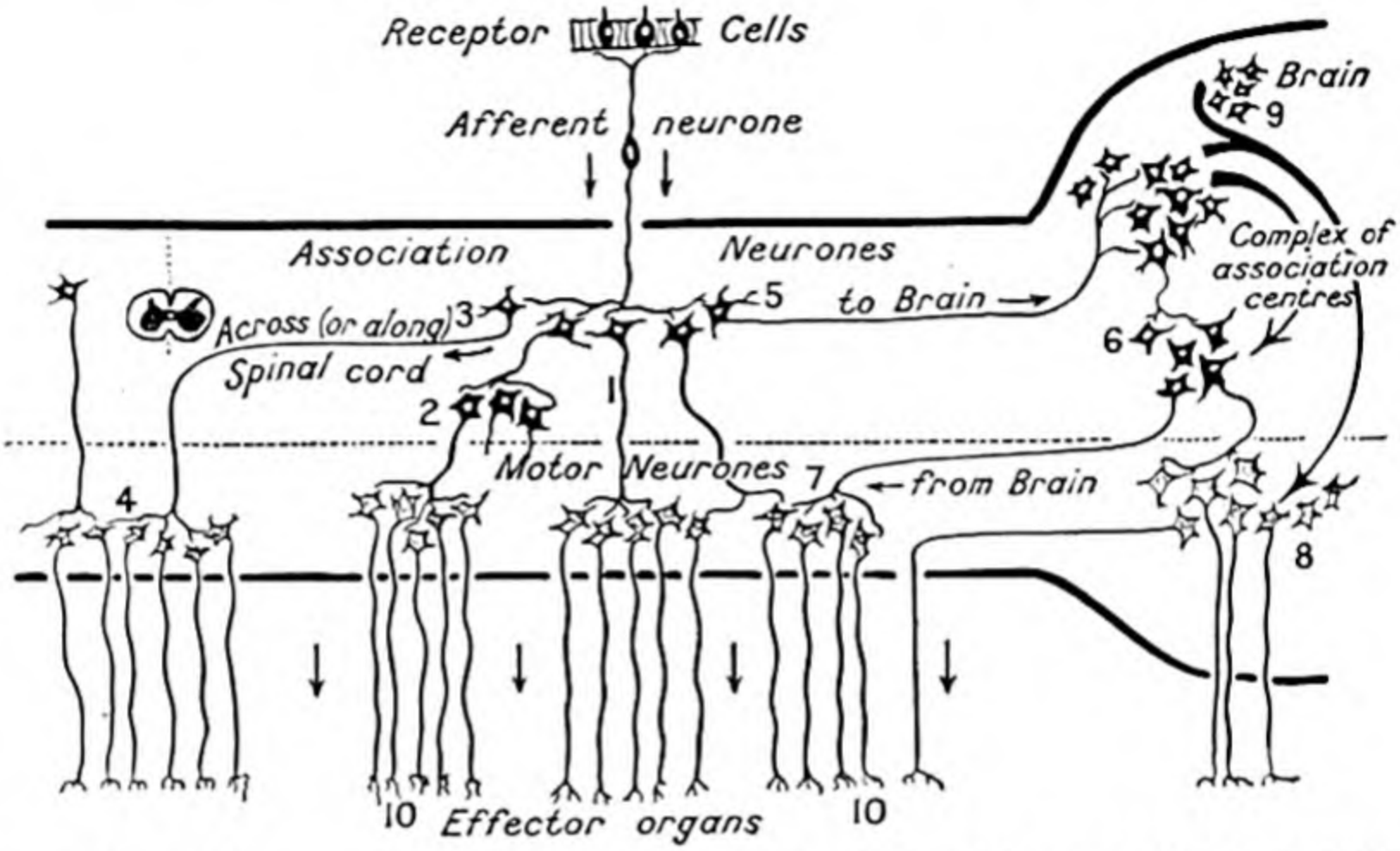


FIG. 281 – Diagram to show the role of Association Neurones in the nervous system. (Note the multiplication and spread of impulses at the synapses.)
(1) Basic pattern – one association neurone contacting several motor neurones.
(2) Secondary association neurones – increasing the spread.
(3) Association neurone conducting along (or across) the spinal cord and stimulating motor neurones (4), which may also be stimulated by association neurones of their own area.
(5) Association neurone conducting to (6) – complex association centres in the brain.
(7) Stimulation of motor neurones from both spinal and cranial association neurones.
(8) Cranial motor neurones.
(9) Higher centres of cerebral cortex, capable of initiating impulses without reflex stimulation.
(10) Effector (motor) organs.

presumed in actual fact to create not a single impulse in an individual fibre but a volley of impulses in many fibres. Each sensory fibre, in its turn, is known to form synaptic connexions, via association neurones, with several motor fibres, whilst every motor fibre is similarly connected with the terminal arborisations of several sensory fibres. This state of affairs is illustrated diagrammatically in Fig. 281. It is probably the simultaneous arrival of several sensory impulses converging upon a motor neurone which results in the activation of the latter. Thus it becomes

clear that the response to a single stimulus may well be modified by the occurrence of neighbouring stimuli, the single stimulus being only one part of the total pattern of collective response. Particularly is this true in relation to the regulatory effect exerted by the brain in motor response. In mammals there is a definite line of communication – *the pyramidal tract* – between the neurones of the cerebral hemispheres and the motor neurones of the spinal cord, so that, at any one time, the motor neurones are subjected to excitatory or inhibitory influences, thereby determining their final response to external stimulation. Readers who wish to delve more deeply into this problem are advised to read the illuminating article entitled *The Functions of the Central Nervous System*, by Prof. J. Z. Young, in *New Biology*, *No.* 1 (Pelican Books).

Proprioception

When voluntary muscles are involved as the effectors in the com-

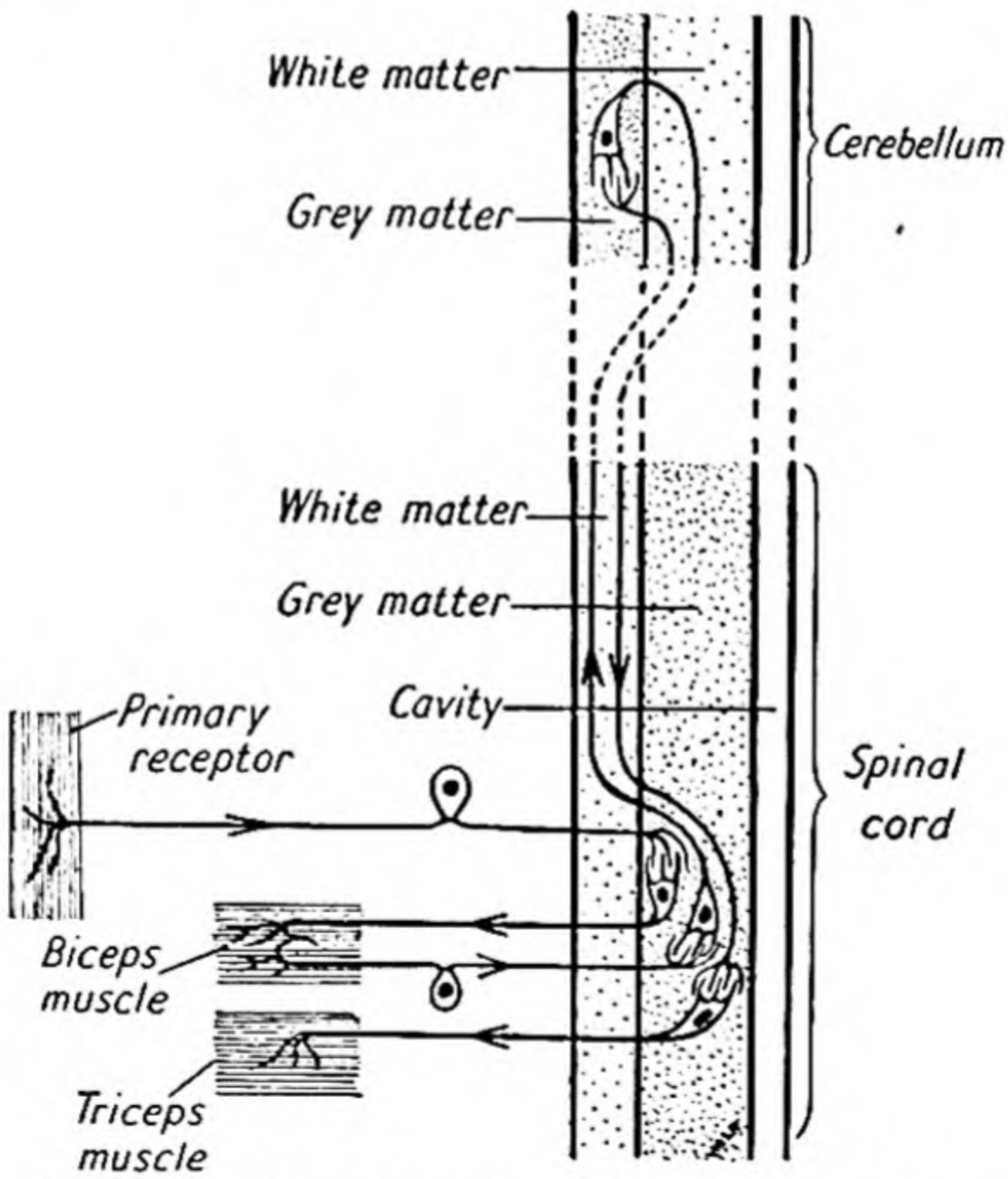


FIG. 282 – Diagram to show the path taken by a nervous impulse through a proprioceptive arc.

pletion of a reflex action a new phenomenon must be taken into consideration. Voluntary muscles are arranged in the body in antagonised pairs,

each opposed in its effects to the other. Thus, for example, the biceps and triceps muscles are antagonised, the former being responsible for the flexure of the arm at the elbow and the latter for its straightening out. As one of these muscles is stimulated to contract the other must undergo a positive relaxation to permit movement: more than a passive stretching of the opposite number is involved. This co-ordination between muscles is under nervous control, the paths involved comprising an important component of the **proprioceptive system**, of which the cerebellum might be regarded as the headquarters.

Suppose that a stimulus is applied to the hand as a primary receptor, resulting in the contraction of the biceps muscle. The instant this contraction commences a new impulse is generated, so that the biceps muscle becomes now a secondary receptor. The impulse follows the path indicated in Fig. 282, passing up an association neurone to the cerebellum and returning to the level of the arm similarly. A motor neurone then conveys the impulse to the triceps muscle, which thus becomes a secondary effector, being stimulated to relax. Thus free movement of the arm is permitted. The neurones involved between the biceps and triceps muscles constitute the proprioceptive arc. The importance of such co-ordination between muscles becomes apparent when it is realised how closely not only antagonised muscles of the same limb, but also muscles of opposite limbs, must be correlated in the simple act of walking, for example.

Autonomic Nervous System

Reference has been made on occasions to the autonomic component of the nervous system, and its structure and function will now be considered.

It consists essentially of two sets of neurones – the **autonomic** and the

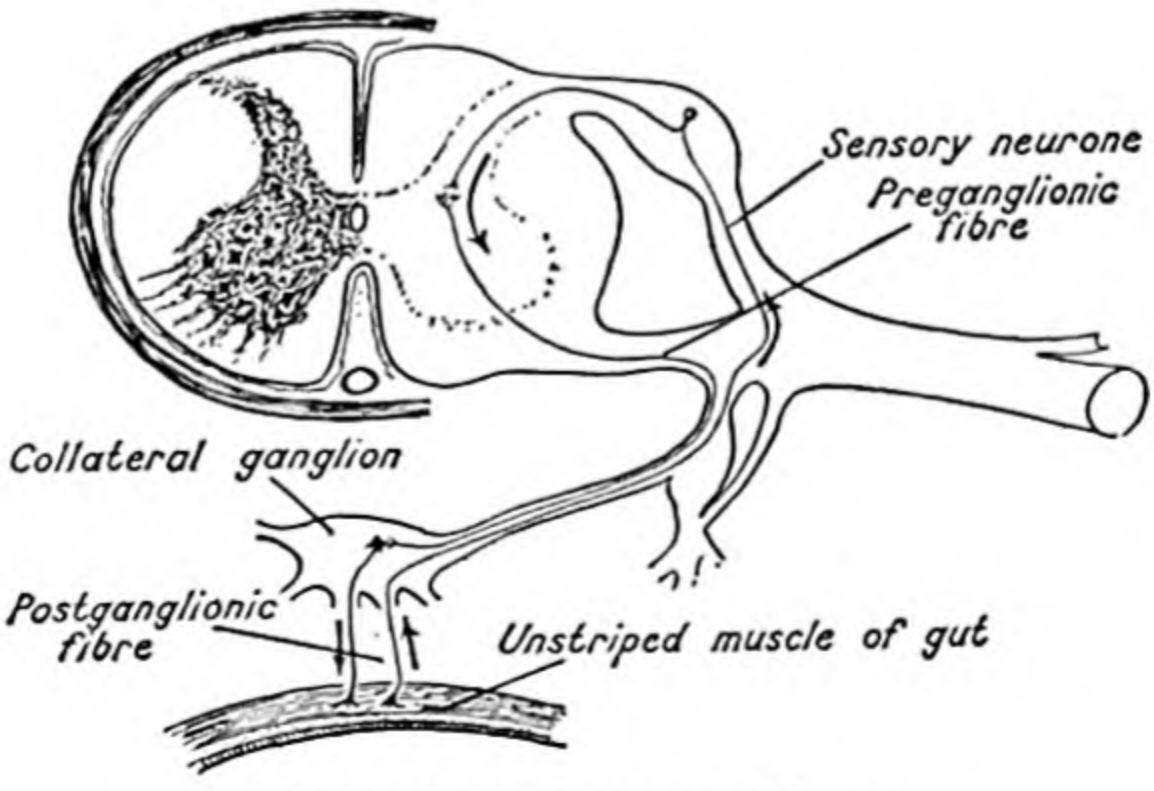


FIG. 283 – Simple visceral reflex arc.

connector. The cell-bodies of the former lie in ganglia, whose disposition will be detailed below, and receive impulses from the spinal and cranial nerves via the *rami communicantes*, already mentioned on page 133. A careful study of Figs. 283 and 284 will be of great assistance in following the possible paths taken by these neurones to and from the ganglia. It will be observed that, in general terms, impulses, originating mainly in the viscera, reach the grey matter of the spinal cord along afferent neurones, and here synapses are established with the cell-bodies of the connector neurones. These pass outwards along the rami communicantes to the cell-bodies of the autonomic neurones, with which further synapses are established in the various ganglia of the system. Impulses are conveyed from these ganglia along the autonomic fibres to various visceral organs.

The distribution of the various ganglia referred to above is as follows. In the head there is a paired series, connected with the cranial nerves. In the trunk there are two series. One of these is median – the **collateral ganglia** – lying in the mesenteries and on the viscera, the most conspicuous being a fused collection at the base of the dorsal aorta, near the origin of the anterior mesenteric artery; it constitutes the *solar plexus*. The other series is paired and segmental – the **lateral ganglia**. In mammals there is much coalescence of this latter series in the anterior part of the

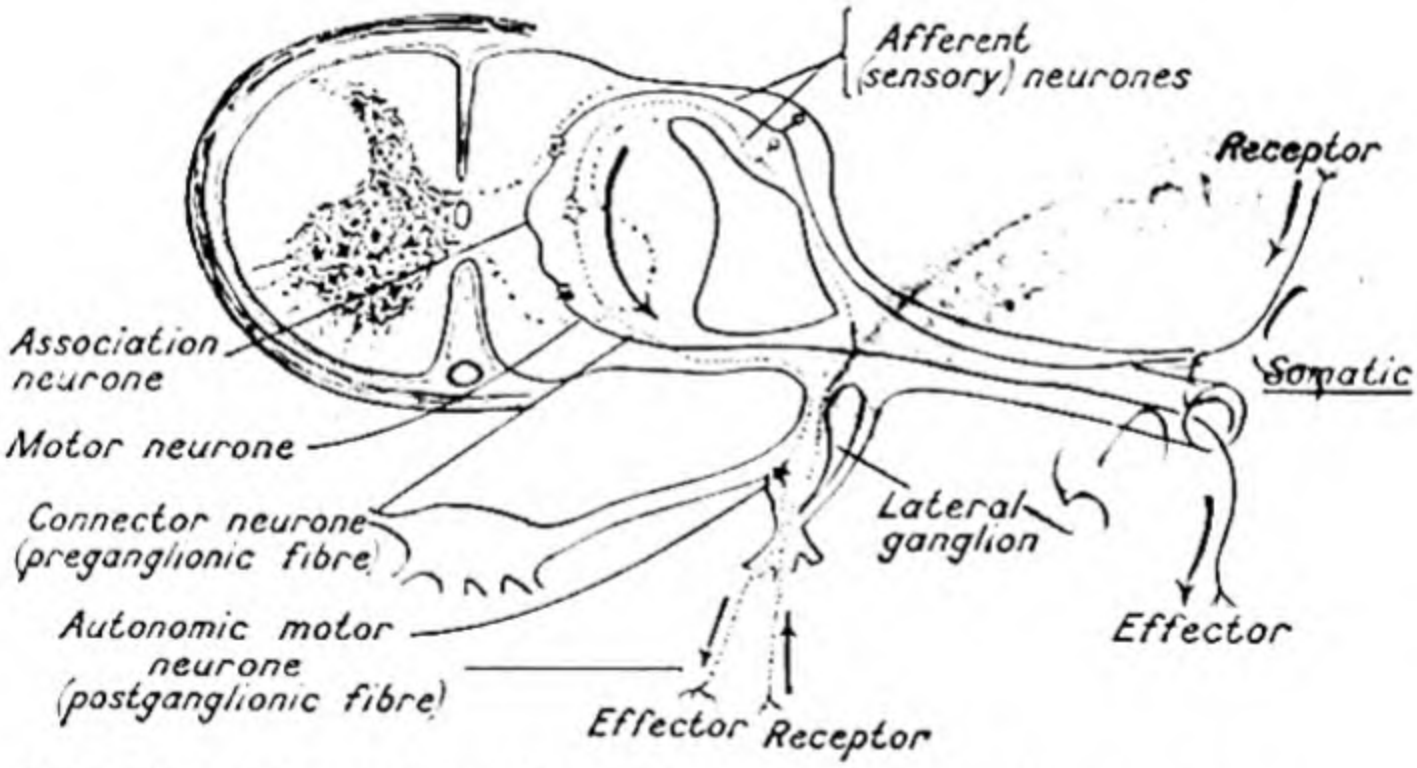


FIG. 284 – Comparison of somatic (—) and visceral (. .) reflex arcs.

trunk, leaving only the **anterior** and **posterior cervical autonomic ganglia** in the neck, and the **stellate ganglia** at the anterior end of the thorax.

The whole autonomic system is often regarded as a complex of two sub-systems – the *sympathetic* and the *parasympathetic*. The fibres of both follow the same course, but are functionally differentiated, the former being excitatory and the latter inhibitory. This is probably true in general, though it would appear that some structures – e.g. the *erector pili* muscles – receive only impulses resulting in excitation. It is, how-

ever, as well to avoid confusion by retaining the term 'autonomic' wherever reference to either type of fibre may be intended. The difference in effects exerted by the two sets of fibres is believed due to the substances liberated from their endings under stimulation. Parasympathetic fibres liberate *acetyl choline*, and sympathetic fibres *sympathetin*. This latter substance is believed to resemble adrenalin, thus accounting for the similarity of the effects of this hormone on the one hand and the stimulation of the sympathetic fibres on the other.

The autonomic nervous system is essentially responsible for co-ordinating external conditions with those obtaining in the organs within the body. Thus, when food enters the mouth the secretion of saliva is stimulated by the passage of impulses along the autonomic fibres associated with cranial nerves V, VII and IX. The sensation of nausea on witnessing an accident similarly results from such stimulation. The original term 'sympathetic' was doubtless applied, in fact, because functionally this component of the nervous system causes the body to react internally 'in sympathy with' prevailing conditions.

Cranial Nerves

Although the first part of this chapter is primarily concerned with the form and function of the nervous system in its own right, it will not be inappropriate at this point, while studying the distinguishing features of cranial nerves, to analyse their distribution in terms of the segmentation of the head of vertebrates, for it plays an important part in the diagnosis. It has already been observed that a typical spinal nerve consists of a dorsal root and a ventral root, working in close association. The former is concerned with the reception of stimuli and the conveyance of impulses to the spinal cord, whereas the latter redistributes these impulses to the musculature of that particular segment. Thus in the trunk segmentation is a fairly obvious phenomenon, since it is manifest in both the disposition of the spinal nerves and the transverse division of the vertebral column into separate vertebrae. But this same phenomenon is by no means so apparent as a result of a cursory survey of the structure of the head. No segmental arrangement is at once demonstrated either by the skull or by the distribution of the cranial nerves.

One characteristic of cranial nerves, in which they differ from spinals, is that each is either a dorsal or a ventral root and they remain so throughout their length. It is to be noted, however, that some cranial nerves contain a mixture of components. By tracing the development of cranial nerves, together with that of related musculature and skeletal structures, it has been found possible to establish the presence of segmentation in the vertebrate head.

The first and second cranial nerves (the olfactory and the optic) are not true nerves, and are therefore of no significance in this respect. No. I is formed by the backward extension of processes from cells constituting

the endothelium lining the nasal chambers. These processes penetrate the olfactory lobes and constitute the olfactory nerves. No. II is formed, as is the whole eye-cup, merely by an outgrowth from the mesencephalon itself.

The first true segment, known as the premandibular, has for its dorsal root the profundus branch of the trigeminal nerve. This disappears in *Scyliorhinus*, but is present in closely-related forms. The ventral root corresponding to this is the oculomotor nerve (III).

The second (mandibular) segment has as its dorsal root the remainder of the trigeminal nerve (V) – i.e. the superficial ophthalmic, maxillary and mandibular branches. Nerve IV (trochlear) is the corresponding ventral root.

The third segment is known as the hyoid, and the facial nerve (VII) supplies its dorsal root, whilst the auditory nerve is regarded as a branch of this. It has for its ventral root the abducens nerve (VI).

The fourth segment has as its dorsal root the glossopharyngeal (IX), whilst the disappearance of the myotome from this segment accounts for the absence of the corresponding ventral root.

The vagus nerve supplies the dorsal roots of the fifth, sixth, seventh and eighth segments. The myotome of the fifth segment disappears, so that, like the fourth segment, this has no ventral root. The ventral roots of the sixth, seventh and eighth segments are provided by the hypoglossal nerve. In the dogfish this is not a cranial nerve, since it arises outside the skull. In reptiles, birds and ammmals, however, its origin comes to lie within the skull, and thus it constitutes the twelfth cranial nerve, whilst the eleventh, known as the spinal accessory, is a specialised branch of the vagus. Thus the ninth segment of the body is the first to have a complete, mixed spinal nerve. It is characteristic of each dorsal root that it bears a ganglion – i.e. the Gasserian, geniculate, petrosal and vagus ganglia of nerves V, VII, IX and X respectively – and it mainly innervates a sensory surface. The ventral roots have no ganglia and each

Segment	Visceral Arch	Gill-slit	Dorsal Root	Ventral Root
1	(Premandibular)		V (Prof.)	III
2	Mandibular	(Mouth)	V (others)	IV
3	Hyoid	Spiracle	VII, VIII	VI
4	1st branchial	1st	IX	—
5	2nd branchial	2nd	X	—
6	3rd branchial	3rd	X + Spinal Accessory (XI)	Hypoglossal (XII)
7	4th branchial	4th		
8	5th branchial	5th		

supplies the musculature of its own segment.

The table on p. 469 will serve as a summary of the facts of segmentation of the vertebrate head. This table, as constructed, largely reflects the state of affairs in *Scyliorhinus*, but at the same time, with appropriate minor adjustments, may be held to indicate the position throughout the whole vertebrate series. For this reason nerves XI and XII have been included.

The Brain

It will be apparent that the spinal cord can receive from the outside world only impulses generated in response to touch. Such stimuli are severely limited in number, for each can be applied only by actual contact with the surface of the body. But at the anterior end of the body are found the sense organs, and these can receive stimuli from a distance. It is true that the sense of smell depends on the contact of the odoriferous substance with the nasal epithelium, but small particles, even molecules, will suffice to bring about the impression of smell, even though the bulk of the substance be an appreciable distance away. Hearing and sight are due merely to vibrations, and can be transmitted for a very great distance. Accordingly the eyes, nasal organs and ears are known as **distance receptors**, since they receive stimuli at a distance from their source. Thus in the central nervous system of this region there have to be received a very great many more impulses than elsewhere, so that accordingly specialised centres are developed which accommodate this demand. The degree of organisation of these centres varies in different classes of vertebrates. In fish and Amphibia decerebration makes relatively little difference to powers of vision, but defects become marked in birds, whilst mammals similarly treated are practically blind. It would appear that in the lower vertebrates the impulses pass directly to the visual centres in the optic lobes, which themselves act as centres for the completion of reflexes. But in higher forms the impulses are conveyed from the optic lobes to the cerebral cortex before connexion with the motor components is established, and this structure increases in importance, and hence in structural complexity, up to the mammals, where it is functionally divisible into clearly defined areas, one of which is associated with vision. In this connexion the paths taken by the nerve fibres passing from the retina to the cerebral cortex in mammals is important. Most herbivores have panoramic vision, the eyes being set wide apart and each receiving a different picture. In these cases the decussation of the fibres of the optic nerves at the optic chiasma is complete, the fibres from each eye passing to the opposite side of the cortex. But in most carnivores, and notably in man, vision is stereoscopic, and the axes of the eyes are converged upon the same visual field. Here the optimum decussation involves only half the fibres from each eye, so that either side of the cerebral cortex receives impulses from the same side of both retinae.

In mammals the function of the corpora quadrigemina is almost entirely confined to visual and auditory reflexes. The upper pair of these bodies, termed the **superior colliculi**, are concerned with visual reflexes, being responsible for the reflexes of the extrinsic eye-muscles and movements of the head and trunk in response to visual stimulation. The lower pair, known as the **inferior colliculi**, are responsible for auditory reflexes in relation to posture, connexions being established between the vestibular apparatus of the ear and the muscles of the neck, trunk and limbs. In this capacity they are assisted by the roof of the mid-brain, just anterior to the corpora quadrigemina, whilst the cerebellum is also involved.

Centres of the Brain

The regions of the brain where these various impulses are received are known as sense centres. Thus, in the dogfish there is but little left of the brain once these centres are removed. Impulses from the skin and ear pass to the medulla, from the eyes to the optic lobes, and from the nasal epithelium to the very large olfactory lobes. There is, however, very little correlation between them. Only the cerebellum remains of any importance. To some extent this organ succeeds in correlating auditory and visual stimuli, for it receives from the ear messages as to orientation of the body in space, from the eye it learns the position of the body relative to external objects, whilst it is also informed of the state of contraction or relaxation of the muscles of the body. Thus the cerebellum regulates posture movements of the body.

In higher mammals – e.g. Man – while learning a complicated motor act, such as skating, the control of the various movements is at first very difficult. But after a little practice the required movements become physically possible, but only with great concentration. If attention is relaxed the necessary control fails, and the movements cease or become unco-ordinated. Gradually proficiency is acquired, when the movements appear to become automatic.

The probable explanation is that, in the early stages, the movements of each muscle-group have to be controlled by detailed 'instructions' from the higher centres of the brain, but when once the movements have been arranged in an orderly sequence the cerebellum takes over, little at a time, the necessary group-control of the muscles. When this state of affairs has been reached all that is needed is a series of suitable impulses of a relatively simple nature from the cerebral cortex to the cerebellum; they are modified in the cerebellum before passage to the muscle-groups.

The cerebellum, then, relieves the cerebral cortex of the need for giving detailed 'instructions' for carrying out acts which are likely to be often repeated. Many such acts will naturally be concerned with equilibration, especially in circumstances which are at first novel – e.g. learning to ride a bicycle.

Correlation Centres

In forms above the fish other correlation centres, in addition to the cerebellum, become well developed. Thus the walls of the diencephalon become thickened to form the **optic thalami**, the floor of the telencephalon forms the **corpus striatum**, whilst the roof of this region becomes very much enlarged to form the cerebral hemispheres (**cerebrum**). Corpus striatum and cerebrum are not normally to be found well represented in the same animal.

The **thalami** receive impulses from all the sense centres, and one of their most important functions is their analysis into pleasurable and painful. Accordingly they determine whether a negative reaction shall result, as an escape from danger, or a positive one, as an advance towards food.

The **corpus striatum** is very important in birds, on account of the part it plays in accommodating the instinctive movements performed by the bird in its migratory habits. The detailed structure of this organ is as much a part of the hereditary constitution of the bird as is the colour of its plumage. The structure of the corpus striatum would appear to be more or less irrevocably determined, and little or no plasticity remains in regard to the formation of alternative synaptic connexions. Thus a bird is capable of carrying out purely instinctive reactions, but to a limited extent only is it able to adapt itself to any novel set of circumstances. Thus it can learn remarkably little by experience.

The **cerebral hemispheres** are almost completely absent in fish. In Amphibia the neurones composing them immediately surround the lateral ventricles. Thus the grey matter, constituted by the synaptic connexions between these neurones, occupies the same position as in the spinal cord. A few of the neurones, however, do migrate towards the surface. In reptiles this migration has taken place to a greater extent, so that there is now a superficial layer of grey matter covering each cerebral hemisphere. This is divisible into three regions, two of which are concerned principally with the reception of impulses from the olfactory lobes. This is no doubt due to the fact that they are the nearest of the sense centres to the cerebral hemispheres. These two centres constitute the **archipallium**, whilst a small region, known as the **neopallium**, receives messages equally from all the sense centres. It is this region which becomes most highly developed in mammals.

The **cerebral cortex**, as the superficial layer of grey matter covering the cerebral hemispheres now becomes known, is but poorly represented in birds. This may be explained on the grounds that they are sufficiently masters of their environment as a result of the very high degree of perfection to which their instinctive behaviour is developed, accommodated by the corpus striatum.

The cerebral cortex is a layer of grey matter covering the cerebral hemispheres and is especially well developed in mammals. It is composed

of neurones, supporting tissue (neuroglial cells) and blood-vessels. In man it forms a much-folded, laminated layer, with an average thickness of about 0.25 cm. and containing approximately 10^{10} neurones. Basically there are two types of neurone – the pyramidal and the stellate. In the former the perikaryon (the cell-body, containing the nucleus) is roughly conical. An apical dendrite is directed towards the surface of the cortex and frequently bears lateral branches, whilst other dendrites arise from the margin of the base. The axon emerges from the centre of the base and it, too, bears branches, some of which may run recurrently, parallel with the axon. Any one cell may bear up to fifty dendritic branches. The stellate cells possess spherical perikarya, and both dendrites and axon may arise from any point on the surface. Though there is much variation in the density of packing of the neurones, partly due to the folding of the cortex, it is estimated that activity in any one cortical cell may well be transmitted to any of 4,000 others. In the light of this almost incomprehensible complexity, the functional interpretation of the known structure of this organ presents great difficulties. The earlier concept of the development of independent circuits is no longer tenable. This is not entirely to deny the existence of preferential paths. Thus, as suggested by Cajal and reitterated by Hebb, if an axon of cell *A* is closely situated to cell *B* and persistently excites it, 'some growth process or metabolic change takes place in one or both cells such that *A*'s efficiency, as one of the cells firing *B*, is increased'. But in the main it is to be visualised that wide fields of excitation exist and that behaviour is dependent upon their *pattern*, rather than upon a number of separate circuits. This is borne out by the lack of uniformity of cortical maps, indicating that precise areas cannot, in general, be identified with specific functions. The fact that childhood experiences are long remembered, whilst recent events in old age are quickly forgotten, is accounted for on the assumption that Cajal's 'growth processes or metabolic changes' can no longer occur.

Whatever effects are produced on the cortex by individual sensory experiences it would appear that those emanating from speech and writing are similar. The ability of man to accumulate in so short a time the experiences of others provides one of his principal evolutionary assets.

More recently it has been suggested that the only true approach to the problem of cortical organisation must be essentially statistical. The behaviour of an aggregate of neurones cannot be understood merely by the study of isolated, single neurones. This is comparable with the impossibility of predicting the behaviour of a crowd of men and women from a study of isolated individuals. Whether atoms, neurones or human beings be involved, the behaviour of aggregates, where interaction occurs, must remain essentially a statistical problem.

For further reading on this fascinating subject the student's attention is warmly directed to *The Organisation of the Cerebral Cortex*, by D. A. Sholl (Methuen).

Movement in Animals and Plants

Contraction of Muscles. Two significant fibrous proteins have been isolated from muscle – *myosin* and *actin*. Myosin is confined to the *A* bands; actin extends from the *Z* bands into the *A* bands. Contraction is believed to depend upon the union between actin and myosin filaments, brought about by the sliding of the latter towards the centre of the sarcomere. Following this, it is believed that intra-molecular changes occur, resulting in the shortening of the filaments. Other authorities maintain that the filaments remain in continuity and that the reversible intra-molecular changes alone are responsible for the contraction and relaxation of muscles.

As a general rule plants are sessile organisms, whilst animals are motile. But to this there are exceptions. Thus many of the non-cellular Algae possess lashing flagella, by means of which they swim, whilst the reproductive bodies of many of the lower plants have some locomotary mechanism. Certain animals lead an attached mode of life, and especially is this feature encountered amongst the Coelenterata. Where movement of an organism as a whole occurs it normally depends on the contractibility of protoplasm. Contraction results only in a change of shape, and not of volume, this phenomenon reaching its climax in the specialised muscular tissues of animals. It will be well at this point to review the organs of locomotion in the principal groups of the animal kingdom.

Locomotory Organs

In the Protozoa pseudopodia may be regarded as the most primitive organs of locomotion, and their mode of action has already been described for *Amoeba* (page 4). In other forms specialised and delicate outgrowths from the body-wall facilitate movement, as seen in the flagella and cilia. A contractile layer, the myocyte, has been mentioned in connexion with *Monocystis* (page 14).

In all other groups, from the Coelenterata upwards, locomotion is effected by means of muscles. In *Hydra* these take the form of flattened expansions at the inner ends of the musculo-epithelial cells, whilst in *Obelia* the two components have become separated. In most higher forms the muscles accommodate the movements of various structures, collectively termed appendages, and together they effect locomotion. Appendages of a particular group become variously modified according to habitat, and examples will be drawn from insects, birds and mammals.

Flight in insects is accommodated by one or (usually) two pairs of wings. These are membranous outgrowths of the cuticle, thickened along their anterior margins and remaining delicate posteriorly. When they beat downwards the motion of the hind part of the wing is retarded by air pressure, so that the wing strikes the air more or less obliquely, thereby driving the insect forwards as well as keeping it supported. In the bee,

for example, it is estimated that the wings vibrate two to four hundred times a second, so that it is little wonder that the flight of insects is so rapid, even for a creature so small. Where two pairs of wings are present those of each side are normally locked together during flight. *Dytiscus*, the water-beetle, has its posterior pair of legs modified for locomotion in water. They are flattened and expanded, as well as which they bear rows of oar-like, stiff hairs. The animal swims on its ventral surface, a supply of air being collected on occasional ascents to the surface and carried imprisoned beneath the elytra.

Amongst vertebrates fish are characteristically aquatic, and for purposes of locomotion the fins are developed. The tail fin is most important in this respect. It lies in a vertical plane and is moved slowly first to one side and then to the other. From each lateral position it is jerked back rapidly to the middle line, thus propelling the animal. The pectoral and pelvic fins function to accommodate changes in depth. Thus the beating of the pectoral fins will bring the animal nearer to the surface, whilst that of the pelvics will exert the reverse effect.

The wings of birds are normally adapted for flight, and in this respect their covering of large, expanded feathers is of great importance. In a few cases, however, birds are aquatic, when their wings are modified to form paddles. They are reduced in size – e.g. the flippers of penguins – and in many cases are not functional for flight. The hind-limbs, too, are adapted to locomotion in water in that the toes are webbed.

Mammals are mostly terrestrial. One or two interesting modifications in their limb-structure may be observed. In the Ungulata (hoofed

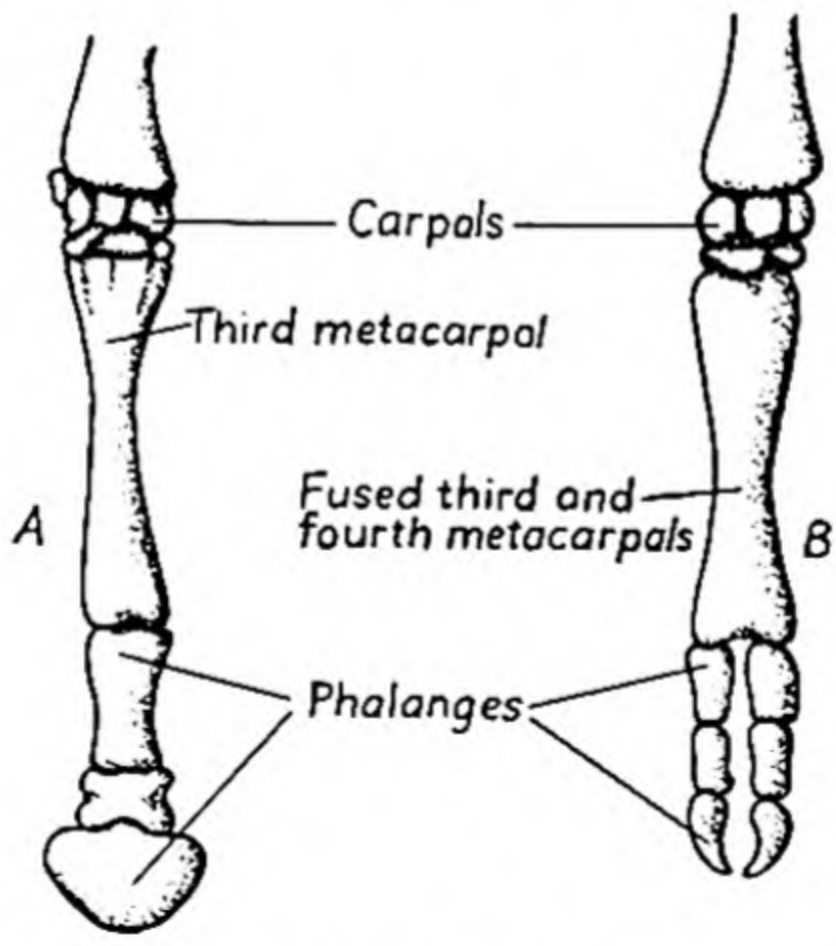


FIG. 285 – Skeleton of the front foot, of *A.*, a horse, and *B.*, a camel.

animals) two independent developments have occurred to facilitate rapid locomotion. In one type, described as **perissodactyl** (odd-toed), the middle digit has become very much elongated, whilst the second and fourth are mere splint bones: digits I and V have disappeared. This condition is exemplified in the horse, and is to be compared with the **artiodactyl** (even-toed) type of limb modification, where digits III and IV are greatly elongated, whilst II and V are variously represented, being vestigial, for example, in the deer and absent in the camel. This may be taken as an excellent example of convergent evolution.

In aquatic mammals the limbs are modified to form paddles, as in the seals, sirenians and whales. They are considerably shortened, whilst there may be more than the normal five phalanges. The whole limb is enclosed in a common skin, thereby offering greater resistance to the water.

Bats are mammals adapted to flight. Digits II and V are greatly elongated to support the membrane forming the wing, the surface of which often bears fine hair. This is in contrast to the condition in birds, where the flying membrane is supported almost entirely by digit II and consists chiefly of feathers.

In all the above cases the movements of the organs referred to are effected by muscles. Even when not actually working, these muscles are never completely relaxed, but are always on the point of contraction. This condition is known as **muscular tone** and is important in maintaining organs in position when at rest. When a muscle is stimulated by a nerve-ending to contraction there is a short lapse of time between stimulus and response. This is known as the **latent period**. It is normally very short, being less than one-hundredth of a second in isolated frog's muscle, for example.

Conduction of Impulses. Impulses travel in the form of electrical waves, normally between 5 and 50 per second in continuous stimulation. Their fastest speed is of the order of 100 m per second. In a resting nerve-fibre the surface is polarized, with a layer of positive ions on the outer surface and of negative on the inner. This is achieved by the far greater permeability of the surface membrane to potassium and chloride ions than to those of sodium. A metabolic mechanism, known as the sodium pump, is also involved, driving out the sodium ions, of which there is, therefore, an excess on the outside of the fibre and a deficiency within, thus setting up a potential difference across the surface membrane. On stimulation the fibre becomes locally permeable to sodium ions, which rush inwards at a rate far too great to be accounted for by the mere failure of the sodium pump. This is accompanied by the egress of potassium ions, though at a speed well below that of the entry of sodium ions. Thus a local current flows and this, in its turn, depolarizes the adjacent section of the fibre. This effect is continued along the fibre. The increased permeability to sodium ions is short-lived, and following this the permeability to potassium ions is increased. Thus the nerve-

fibre becomes repolarized. During this phase, known as the *refractory perion*, a second impulse cannot be passed. In view of the similarity between sodium and potassium ions, it is likely that the differential permeability referred to above is due to their being carried as different complexes attached to organic molecules.

Movement of some parts of an organism relative to others is encountered in both animals and plants. It is sufficiently obvious in animals to need no further elaboration here, but the movement of certain parts of plants must be considered in more detail. In this connexion the phenomenon of photonasty may be briefly described, whilst a further aspect of phototaxis may be mentioned.

Photonasty is the response by plants, or part of plants, to diffuse light, in which case the resultant movement bears no relation to the direction of the incident rays. The most obvious example of this is afforded by the 'sleep' movement of leaves and flowers. In general they owe their occurrence to the greater quantity of light present during the daytime, though the higher temperature of this period may also exert some effect. Petal movements are usually regarded as due to unequal growth on the two sides, whilst those of leaves occur as a result of changed turgor of cells in the region about which the leaf rotates. The influence of light in retardation of the rate of elongation and the production of etiolation has already been described (page 420). This may properly be regarded as one aspect of photonasty.

As well as causing the movement of motile plant bodies, light is effective in producing changes in position depending primarily on the intensity of illumination. The chloroplasts are, in fact, said to be phototactic. Thus in the duck-weed, for example, the chloroplasts come to lie parallel to the surface of the leaves in moderately strong light, but should the illumination become intense they will migrate to take up a position at right-angles to the surface. In darkness they lie scattered throughout the cell. The same is true of land plants, where the chloroplasts congregate at the upper and lower end of the cells of the palisade tissue if moderate light is directed at right angles to the epidermis, but they move to the vertical walls if brilliantly illuminated.

PRACTICAL WORK

'Avoiding' reaction

This may be attempted as directed in the text.

Geotropism

Germinate some peas or beans and lay them on a table for half an

hour with their radicles in a horizontal position. Mark the upper surface with ink. Plant them immediately in damp sawdust with the roots vertical, and examine again a day later. It will be found that the radicles have curved away from the marked (upper) side, showing that they had been geotropically stimulated.

Phototaxis

Introduce into a beaker enough motile Algae – e.g. *Chlamydomonas* – to give a green colour to the water in which they are contained. Cover the beaker with brown paper except for a small slit about a quarter of an inch long. Place in bright sunlight. Examine a few hours later, when it will be found that the Algae have collected in the region illuminated through the slit.

CHAPTER 27

Hormones

In the preceding chapter the function of co-ordination by physical means in animals, involving the perception of stimuli, the transmission of impulses and the final responses, was analysed. There can be no doubt of the importance of this in the life of the animal, for it is so rapid as to occasion almost immediate reaction by the organism to external (and occasionally internal) conditions. But there is another method, well known amongst vertebrates and demonstrated in some invertebrates. It is a chemical method and involves the secretion by special glands, termed **endocrine organs**, of specific substances, known as **hormones**, or **autocoids**. Endocrine organs differ from the more familiar type of gland in that they do not possess ducts. In consequence the products of their activity have to escape by diffusion, usually into the blood-stream, but occasionally directly to neighbouring tissues – e.g. from one lobe of the pituitary (page 484) to another. Depending, as they do, upon diffusion, hormones must be substances with small molecules. Indeed, it has been found that all those so far isolated have low molecular weights. By nature, hormones are typically protein or lipide, and those reaching the blood-stream are distributed to all parts of the body. They are thus able to evoke a response by a tissue or an organ far removed from the seat of origin. Little is known about the exact means whereby a hormone stimulates an organ; it has been suggested that they may have some influence upon the plasma membranes of cells. Different hormones evoke quite different responses, which may fall into any of the following categories –

(*a*) Special organs or tissues (e.g. glands or muscles) may be excited or inhibited.

(*b*) The rate of metabolism as a whole may be modified.

(*c*) One phase of metabolism alone may be affected.

(*d*) A lengthy, slow process, such as growth, may be controlled.

The influence of a hormone, were it a highly stable substance, would continue indefinitely, due to its persistence in the blood. But hormone activity is of limited duration, since hormones are relatively unstable and readily undergo oxidation. Thus sustained hormone action has to be accommodated by sustained secretion. Not all endocrine glands are definite organs, with limiting structural boundaries, but some, lying, for example, in the intestinal mucosa, are scattered groups of cells. Hormones share with the nervous system the task of co-ordination of the various tissues and organs of the body. Likening nervous integration to

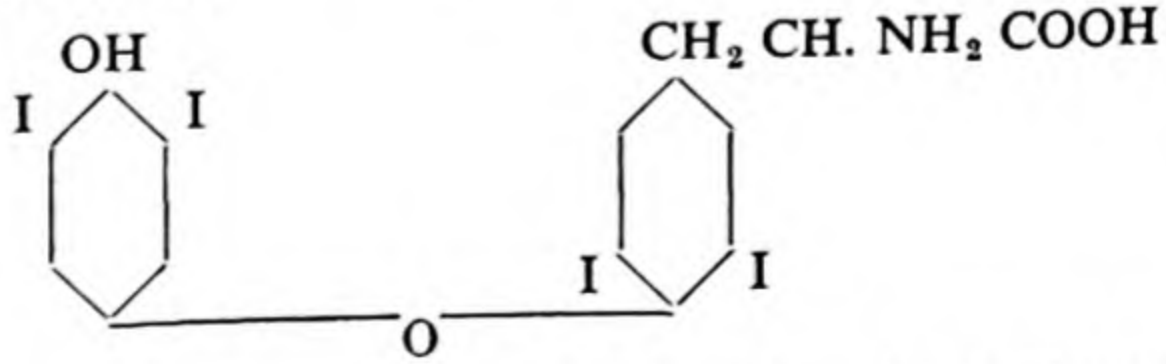
the use of the telephone, the activities of hormones are comparable with communication by letter post. The time lag between the secretion of a hormone and the exercise of its influence is far greater than that between stimulus and response nervously promoted. This is manifestly due to the slowness of blood circulation compared with the high speed of conduction of impulses by nerves. Endocrine organs are themselves co-ordinated either by nerve impulses or by interaction with other hormones. Collectively, endocrine organs produce a hormone complex in the blood and this may be held to constitute a sort of internal environment in which the life-processes of the animal have to continue. It is changes in the balance of this complex, rather than in the amount of a particular hormone, which influence the body. Although investigated mainly in the vertebrates, the presence of hormones in the invertebrates has been conclusively demonstrated.

More recently analogous substances in plants have been discovered. They resemble the hormones of animals in that they do not produce their effect exactly in the region where they are formed, nor are they carried along special channels or ducts. They are distributed partly in the xylem and partly in other tissues of shoot and root from the tips of these organs, where they are secreted, to the region some distance behind the tips, where they are effective. On account of this general resemblance these substances in plants are also termed hormones. Having therefore noted the fundamental characteristics of a hormone, it is necessary for the individual hormones of animals to be studied, after which some indication will be given of present-day knowledge of analogous substances in plants.

Hormones of Animals

In the following pages a knowledge of the structure of the endocrine organs will be assumed, since their nature and position in the dogfish, frog and rabbit has already been described (pages 108, 137 and 176).

THYROXIN. This is the hormone produced by the thyroid gland. It has been extracted and prepared in pure form, and its composition has been determined as:



It appears that the cells of the thyroid gland have the ability to accumulate iodine. In fact, using radio-active iodine it has been shown that as much as 50% of it is accumulated in the thyroid gland. This iodine is employed for converting the amino-acid *tyrosine* into *di-iodotyrosine*,

aided by the enzyme *tyrosine iodinase*. The di-iodotyrosine is then oxidised to thyroxin.

This hormone functions to control the general metabolic rate, which may be increased by as much as 3% in a man by 1 mg. of thyroxin. In this connexion it plays an important part in the regulation of body-temperature, acting in conjunction with the pituitary gland. In cold conditions this latter produces additional *thyrotropin*, a hormone which, in its turn, stimulates the thyroid gland to increase its output of thyroxin, thus raising the metabolic rate and hence body-temperature. It is interesting to note that thyroxin itself depresses the output of thyrotropin. When, therefore, in man, the thyroid gland does not function adequately it becomes over-stimulated by the excess of thyrotropin and hence enlarges: this condition is goitre and is often associated with lack of iodine in natural foods. Shortage of thyroxin in the adult brings about myxoedema, a condition characterised by the patient's becoming fat, bald and sluggish. In a child the condition produced is known as cretinism, symptomised by general under-development, and especially by loss of control over motor organs. In presence of excess thyroxin the metabolic rate in man is increased, whilst nervous disorders and skin pigmentation occur. It can be cured by the administration of thiourea and allied substances, which appear to counteract the effects of the thyroxin.

Less is known about the action of thyroxin in lower vertebrates. In Amphibia it regulates metamorphosis. Thyroidectomy (i.e., removal of the thyroid gland) in a tadpole does not check growth, but prevents metamorphosis, whilst if normal tadpoles are fed on thyroid extract metamorphosis is precocious. In fish, variations in metabolic rate due to temperature changes may possibly be caused by fluctuations in the activity of the thyroid gland. In the case of some fish with complex life-histories it has been found that changes from one stage to another often coincide with hyperactivity of the thyroid gland. Examples are provided by the transition from parr to smolt in salmon and from larva to elver amongst eels. It has been suggested in this connexion that thyroxin is of osmo-regulatory significance.

PITUITARY GLANDS AND ITS HORMONES. Although in this chapter attention is, in the main, concentrated upon the hormones produced by the endocrine organs, rather than upon the structure of the glands themselves, the complex origin, structure and function of the pituitary gland makes it advisable for the various aspects to be taken together, for each is so closely related to the others.

The pituitary gland is of composite origin, arising by the close association of an evagination from the floor of the diencephalon, constituting the **infundibulum**, with an evagination from the roof of the buccal cavity, known as the **hypophysis**. Further differentiation results in the subdivision of the adult gland into four parts. Derived from the infundibulum is the *pars nervosa*, whilst the *pars anterior*, the *pars tuberalis* and

the *pars intermedia*, collectively known as the *pars buccalis*, arise from the hypophysis. The relationships of these parts will be clear on examination of the vertical section of the gland, shown in Fig. 286. The components of the gland are usually further classified, on functional grounds,

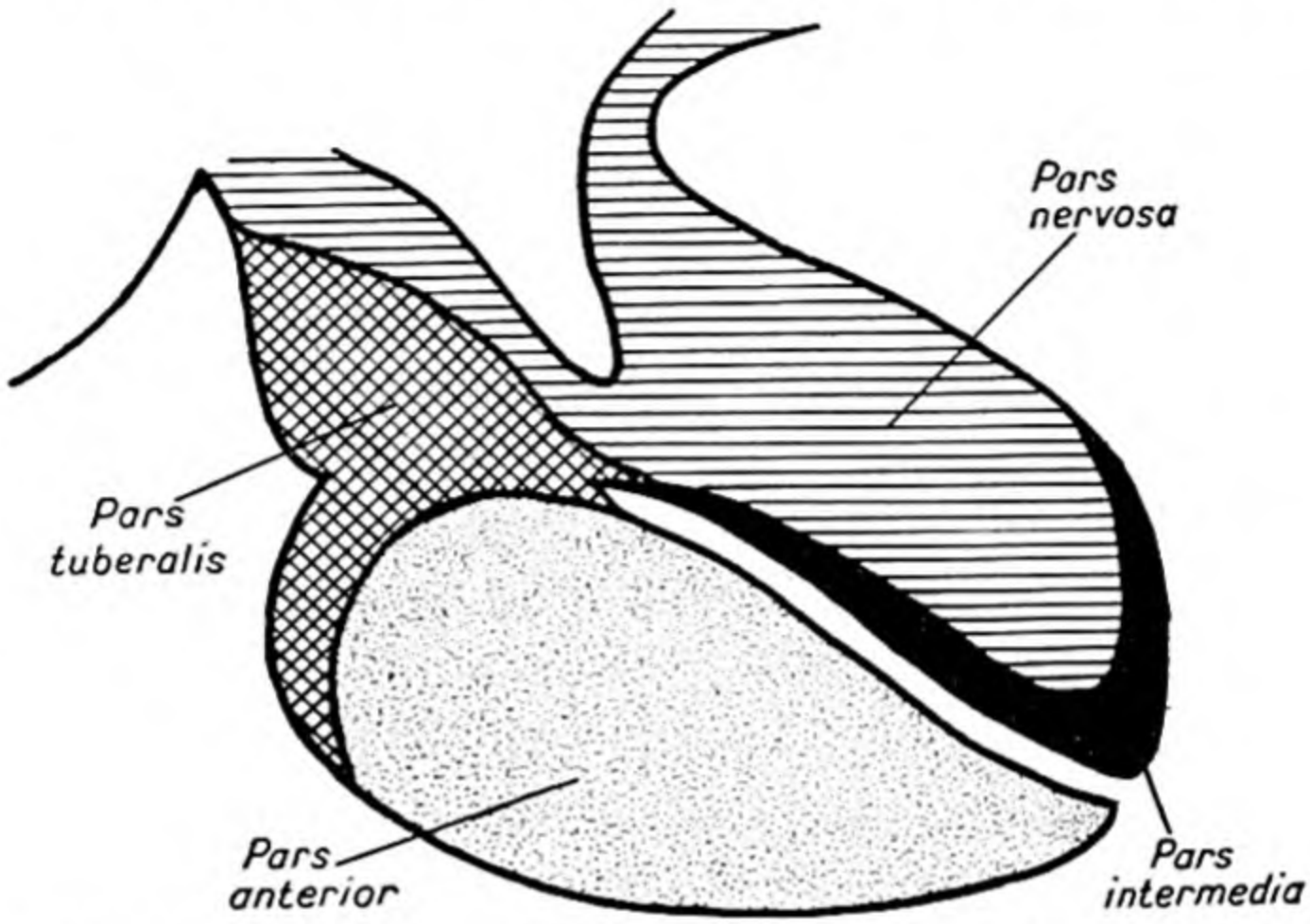


FIG. 286 – Diagrammatic vertical section of the pituitary body of a mammal. (After Grove and Newell.)

into an *anterior* lobe, consisting of the pars anterior and pars tuberalis, a *posterior* lobe and an *intermediate* lobe. Its hormones are, perhaps, best classified according to their seat of origin.

(1) *From the Anterior Lobe.* This section of the gland produces many hormones, the more important of which are mentioned below.

(*a*) *Phyone.* This hormone stimulates the growth of the long bones. Lack of it results in dwarfism and excess in gigantism. It can be administered only by injection, and such injection can be of value only before the bones have passed their period of growth. Over-production of phyone by the pituitary body after the bones have reached their full length results in acromegaly, symptomised by the distortion of the skeleton and the assumption by the face of a massive and angular form.

(*b*) *Gonadotropic Hormones.* These are distinct in male and female. In the male deficiency of this hormone results in failure of testes to produce the characteristic testicular hormone (see later), in consequence of which secondary sexual characters do not appear, whilst spermatogenesis is suppressed.

In the female the gonadotropic hormones are responsible for the maintenance of the oestrous cycle and there is an interesting case of relationship between these hormones and those of the ovary. The oestrous cycle may be regarded as a complex of two cycles – the *ovarian* and the *uterine*.

Considering the ovarian cycle first, a follicle-stimulating hormone (*FSH*) *from the pituitary* promotes follicular growth and maturation, being operative just before menstruation. Following ovulation, another *pituitary hormone*, known as the luteinizing hormone (*LH*), stimulates the development of the corpus luteum (page 488), which itself soon disappears unless pregnancy intervenes. Turning now to the uterine cycle, there are two distinct periods of hormonic influence upon events. In the period of *follicular* influence an oestrogen (see page 487) liberated from the developing follicles causes marked changes in the wall of the uterus, where the cells of the mucous membrane proliferate rapidly and the lining becomes thick, spongy, glandular and vascular, all in adaptation to possible pregnancy. This same oestrogen also suppresses the production of *FSH*. In the period of *corpus luteum* influence the hormone *progesterone* from this gland further inhibits the production of *FSH* and *LH* by the pituitary, whilst it maintains, and even enhances, the effects of the oestrogen on the uterine wall, causing the glands there to become functional.

Should pregnancy occur, a hormone liberated by the chorionic tissue (see page 543) of the implanted embryo passes into the blood-stream of the mother, where it exerts the same effects as does the *LH* of the pituitary. Its continued secretion during pregnancy maintains the corpus luteum working to full capacity, with the result that events of the oestrous cycle are suppressed, whilst the body of the mother becomes organically fitted for its current function. If, through the failure of pregnancy, the corpus luteum disintegrates, then the supply of progesterone ceases and the lining of the uterus deteriorates, to be cast out, together with the unfertilised egg, at the next menstrual flow. At the same time restrictions on the production of *FSH* and *LH* are lifted, leaving all ready for the start of a new cycle. The total length of the oestrous cycle is about twenty-eight days, of which about five are occupied by the menstrual flow. Gonadotropic hormones are of importance in the male also. Thus the hormone, known as *FSH* on account of its influence in the female, is, in the male, responsible for the growth of the germinal epithelium, inducing spermatogenesis. The hormone known as *LH* stimulates the interstitial cells of the testis to secrete testosterone (page 486).

(*c*) *Thyrotropic Hormone*. Reference to the interaction of thyroxin and thyrotropin has already been made (page 481).

(*d*) *Prolactin*. This hormone, in combination with the progesterone of the corpus luteum, is responsible for the continued secretion of milk by the mammary glands, as well as for maternal behaviour. Thus, if injected into virgin rabbits it induces nest-building.

(*e*) *Pancreatropic Hormone*. The relationship between this hormone and insulin (see above) is somewhat obscure. Removal of the pituitary relieves the symptoms of glycosuria (sugar in the urine) in a pancre-

atectomised mammal, whilst in the Houssay dog, which has neither pancreas nor hypophysis, injection of the pancreatropic hormone induces hyperglycaemia (excess sugar in the blood). It would appear that this hormone and insulin exercise a restraining influence upon each other's activities.

(*f*) *Adreno-cortico-tropic Hormone*. This hormone, known as *ACTH* stimulates the production of the cortin of the adrenal cortex. Injection of this hormone produces the same clinical results as does that of cortisone. Although *ACTH* has been extracted from the pituitary glands of pigs, it is a very expensive and elaborate process, requiring the pituitaries of some five hundred pigs to provide one gramme of the hormone.

(2) *From the Posterior Lobe*. The hormone produced by this lobe was formerly known by the name *pituitrin*, but the lobe has since been shown secrete a number of independent hormones.

(*a*) *Oxytosin*. This hormone stimulates the contraction of plain (unstriped) muscle, including that of the uterus during parturition.

(*b*) *Vasopressin*. This hormone is responsible for the raising of the blood-pressure, causing the heart-beats to be slower, but more powerful. It also exerts an inhibitory effect upon normal diuresis.

(*c*) *Anti-diuretin*. This causes the renal tubules to remove water from, and so concentrate, the glomerular filtrate, thus conserving water. Its improper functioning leads to polyurea (excessive urine production).

(3) *From the Intermediate Lobe*. The hormone from this lobe causes an expansion of the pigment cells in reptiles and Amphibia, but its effects, if any, in man are unknown.

It was formerly customary to regard the endocrine system as self-supporting and largely independent, with the pituitary gland acting in a sort of supervisory capacity, regulating the activities of other such glands. Several examples quoted above will make it clear that the relationship which does, in fact, exist between the pituitary and other endocrine organs is one of equal partnership, rather than one of master and servant. More important still, it is now quite firmly established that the pituitary itself is under the control of the brain, though this control is differently exerted in respect of the two lobes. The secretory cells of the posterior lobe of the gland are connected by a band of nerve fibres – the *hypothalamic tract* – with a group of special cells in the brain. The latter constitute the *supra-optic centre*, being situated just above the optic chiasma, and may be variously stimulated. Thus, for example, a rise in osmotic pressure of the blood stimulates certain vesicles in the supra-optic centre and impulses to the secretory cells cause production of more anti-diuretin, so that water is conserved. The production of other hormones from the posterior lobe is similarly controlled, though the initial stimulus may be different – e.g., expectation of milking in cattle leads to the ready delivery of milk from the mammary glands, a process governed by a hormone from the posterior lobe of the pituitary gland.

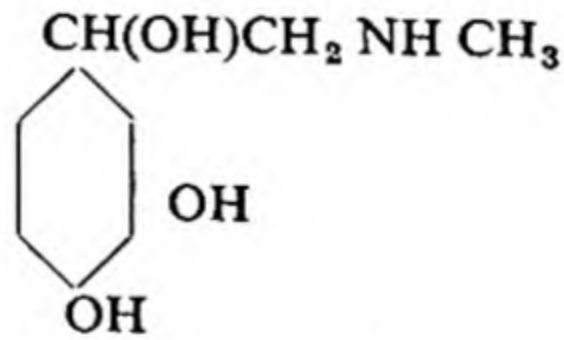
But there is no similar nerve tract serving the anterior lobe. The existence of a series of very fine portal blood-vessels has been demonstrated, conveying blood from the hypothalamus to the anterior lobe of the pituitary, and it is presumably in this way that a functional connexion (of a chemical nature) is established between brain and gland. Thus the pituitary itself is closely regulated by both the brain and other glands, and although it interacts with the latter it cannot be said to exert a one-way control over them.

ADRENAL HORMONES. The adrenal body is a composite structure, consisting of a mesodermal **cortex** and an ectodermal **medulla**. Each of these regions elaborates a specific hormone.

(*a*) *Cortin.* This is the product of the adrenal cortex. In normal circumstances cortin appears to be responsible for much salt equilibrium between blood and kidneys, especially in respect of the elements sodium and potassium, as well as for some stages of carbohydrate and protein metabolism.

The removal or pathogenic destruction of the cortex is the cause of the symptoms of Addison's disease, including extreme weakness, digestive disorders, low blood-pressure and a bronzing of the skin. Cortin is itself a complex mixture of many substances, essentially steroidal in nature. One of the fractions isolated is a substance known as *cortisone*, the injection of which into sufferers from severe rheumatism and arthritis produced such spectacular results that the patients were walking without pain or discomfort after only a few days' treatment. Unfortunately some undesirable effects accompany the administration of cortisone, including increase of blood-pressure, skin eruptions and diabetes.

(*b*) *Adrenalin.* This hormone, secreted by the adrenal medulla, has been both isolated and analysed. It has the chemical constitution:



When injected into the blood-stream it causes the contraction of the arterioles, with increased rate and force of heart-beat. The broncheoles dilate and liver glycogen is converted rapidly into glucose, whilst the pupils enlarge and the saliva becomes viscid. It should be noted that these same effects are produced by suitable stimulation of the sympathetic component of the autonomic nervous system. The natural day-to-day significance of the secretion of adrenalin is unknown. It has often been suggested that it is responsible for the physical accompaniments of emotional stress, and hence primes the organism in times of emergency.

It may well be that these symptoms are first produced by the stimulation of the sympathetic nervous system by prevailing circumstances, and that the increased secretion of adrenalin, promoted by the same source of stimulation, sustains the effects over a longer period.

THYMUS HORMONE. The thymus gland decreases in size with the advent of puberty, and little is known of the function of its secretion. Should it persist in man the patient will exhibit hyper-sensitivity and emotionalism. In birds it controls the formation of the shell and shell-membranes of the eggs.

PARATHYRIN. The parathyroid glands, four small bodies situated dorsal to the thyroid or even embedded in it, are responsible for the regulation of calcium and phosphorus metabolism by virtue of the hormone, *parathyrin*, which they secrete. If, for instance, there is a fall in serum calcium, the gland is automatically stimulated by this very fall to secrete more hormone, thus causing the serum calcium to rise again to its normal threshold value. Deficiency of this hormone causes a lowering of the calcium content of the blood and a marked increase in the amount of phosphorus, leading to muscle tetany and death. If present in excess the consequent increased concentration of the calcium ion in the blood brings about drowsiness and diarrhoea, as well as a marked increase in the viscosity of the blood itself. This increase in calcium concentration is primarily due to the fact that none is eliminated in the urine, nor is it otherwise withdrawn from circulation – i.e. it is not used for the hardening of bones or teeth. Such bones fracture easily and are slow to heal.

INSULIN. Insulin is secreted by the microscopic patches of endocrine gland distributed throughout the pancreas and known as the **islets of Langerhans**. Its presence is essential for the promotion of the proper storage of carbohydrate material in the liver, and for its disposition in the muscles. In absence or deficiency of insulin the carbohydrate concentration of the blood rises, for this hormone is normally responsible for the reduction of this concentration. Its exact mode of action is uncertain, but it probably assists the cells in some stage of glucose respiration. When the sugar concentration in the blood rises above normal the condition known as diabetes results, and the urine becomes sugary. Furthermore, a considerable quantity of sugar may escape in solution in the sweat, crystallising out as evaporation occurs. This condition used to be thought due to a disease of the islets of Langerhans, but recent work appears to indicate that in man the accumulation of sugar in diabetes is provoked by the malfunctioning of the pituitary body. The injection of insulin thus removes the symptoms of a more deep-seated disease.

SECRETIN. When the acidified food passes from the stomach into the duodenum the walls of the latter organ are stimulated to secrete a hormone, known as **secretin**. This is conveyed in the local bloodstream to the pancreas, which is caused to liberate pancreatic juice.

GASTRIN. The early products of digestion in the stomach stimulate

the lining of that organ to secrete a hormone, *gastrin*. This passes into the blood-stream and eventually reaches the gastric glands to evoke the secretion of gastric juice.

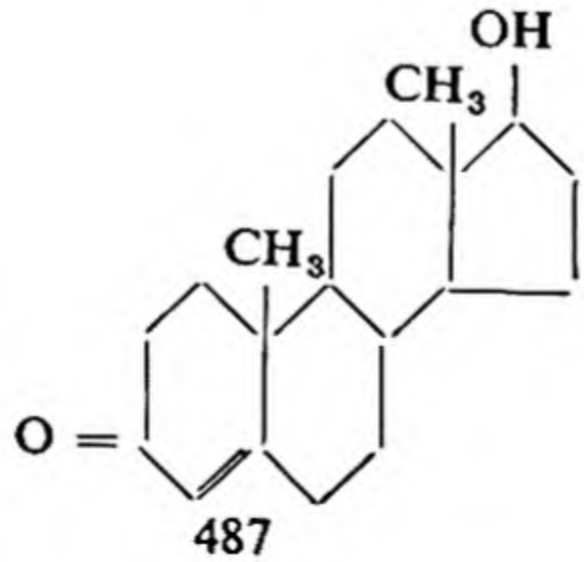
CHOLEOCYSTOKININ. This hormone is produced in the walls of the early part of the small intestine. It is conveyed in the blood-stream to the gall-bladder, which it stimulates to contract, resulting in the discharge of bile along the bile-duct.

ACETYL CHOLINE. Though the function of the spleen is primarily one of manufacture of white blood-corpuscles, it is also believed to be the source of a hormone, termed **acetyl choline**, which has a marked depressor effect on the circulation of the blood.

HORMONES OF THE GONADS. The ovaries and testes, as well as producing germ-cells, give rise to hormones responsible for the development of secondary sexual characters. That some at any rate of these hormones are present prior to puberty, or even to birth, is clearly indicated by the occasional production of a 'free martin' almongst cattle. When twin cattle are born they develop normally if both of the same sex. But if of opposite sexes the male undergoes normal development, whilst the female becomes masculinised. This can be accounted for only on the assumption that the male hormone has been carried in the placental blood-stream to the female foetus, where it produces sexual disturbances. This hormone is probably different from the one liberated at puberty in the male to occasion the appearance of secondary sexual characters. Removal of the testes (castration) at an early stage prevents the formation of these attributes of sexual maturity. Thus in mammals the male and female hormones differ qualitatively.

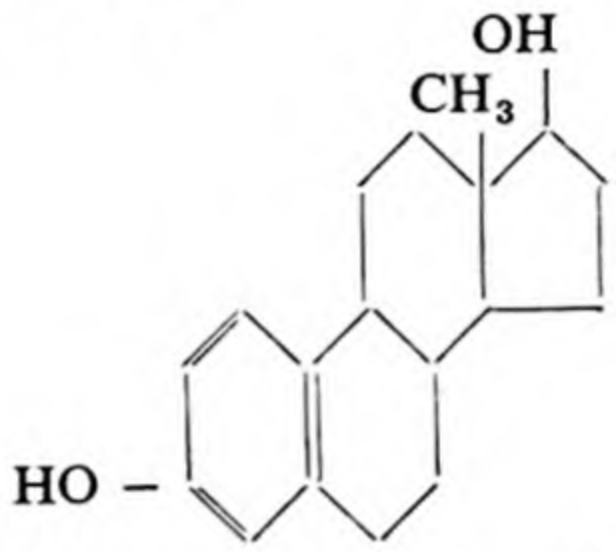
These hormones, responsible for the development of secondary sexual characters, including the initiation of the sex cycle in the female, are collectively termed **androgens** in the male and **oestrogens** in the female.

The principal androgen is *testosterone*, whilst a subsidiary compound – *androsterone* – is derived from it in the body and is to be found in human urine. It may be that it provides means for elimination of excess hormone, which is continuously in production by the interstitial cells of the testis. Both compounds have been synthesised, and the structure of testosterone is –



Several substances have been discovered to have androgenic properties, tested by injection into capons (castrated cocks) and the measurement of subsequent growth of comb and wattles.

Oestrogens are defined as substances which will bring an immature or ovarectomised female on 'heat' (oestrus). Here again two compounds are involved, the principal one being *oestradiol.* with a subsidiary *oestrone.* During pregnancy a third oestrogen – *oestriol* – is found in urine. The elimination of oestrogens in this way may well be important in suppression of the sex cycle at this time. The structure of the oestradiol molecule has been shown to be



Numerous synthetic substances have oestrogenic properties and are of considerable clinical importance.

But in birds the position is somewhat remarkable. Whilst the comb and wattles seem to be controlled by the qualitative nature of the hormones of the two sexes, the plumage depends for its development on the gonads as physiological units, rather than as producers of hormones. The ovary is physiologically more expensive than the testes, and hence the plumage of the female is inferior. That this is so has been forcibly demonstrated by a number of experiments involving gonadectomy and transplantation. Thus if the ovary be removed the plumage becomes that of a male, whilst castration of a male results, if anything, in the improvement of the plumage. Other transplantations are in keeping with these results, and most conclusive of all is the fact that the implantation of additional testicular material into the male results in the deterioration of the plumage to the female type.

HORMONES OF THE CORPUS LUTEUM. When an egg is shed by the bursting of a Graafian follicle the torn tissues on the surface of the ovary become rapidly repaired if fertilisation does not occur. But if the egg is fertilised this region of the ovary becomes enlarged by rapid cell-division and invasion by connective tissue. In this way a ductless gland is formed, known as the **corpus luteum**. The influence of secretions of the pituitary body and chorionic tissue on the activity of this organ has already been mentioned (page 483). The hormone produced by the corpus luteum, known as *progesterone*, fulfils varied functions, all of which are closely associated with pregnancy. It inhibits oestrus (menstru-

ation) and ovulation, it increases the sensitivity of the wall of the uterus and stimulates the mammary glands. After birth it is eliminated in the urine in reduced form as a compound known as *pregnandiol*.

Relatively little is known about hormones in invertebrates, but considerable research has been undertaken into their origin and function in insects. Here there are four distinct sources. (1) *Neurohumours* take the form of active metabolites from nerve-endings. They can be extracted from the brain and other ganglia. (2) *Endocrine organs* arise from ectoderm near the mouth-parts and fragments migrate to a position beneath the brain (*ventral gland*), behind the brain (*corpus allatum*, which may be paired or median), or in the thorax (*thoracic gland*). (3) *Neurosecretory cells* occur in all the ganglia and form specific inclusions which are carried along the axons to be discharged into the blood-stream. (4) *Neurohaemal organs* are the sites of such discharge. The best-known are the *corpora cardiaca*, situated just behind the brain, in close association with the corpus allatum.

Hormones are responsible for the transition from larva to pupa, and from pupa to imago. The *juvenile hormone* from the corpus allatum brings into play several gene groups, according to the amount of it present in the blood-stream. The immediate cause of metamorphosis is the cessation of the supply of this hormone, the effects of which had been to encourage larval development, whilst the subsequent formation of the pupa is due to the presence of only a small amount. Full secretory activity is resumed in the adult and initiates sexual maturity. Polymorphism may likewise depend upon a genetic switch under hormonic influence, the latter being determined by environmental conditions, such as daylight-length, acting via the neurosecretory cells and external receptors.

Hormonic interaction is well illustrated in the control of growth and moulting. Neurosecretory cells release an appropriate hormone following suitable stimulation, which varies with different types of insect. The associated axons cross to run to the corpus cardiacum of the opposite side, there to discharge this hormone into the blood. This reaches the thoracic and ventral glands, which are induced to secrete the hormone responsible for the formation of a new cuticle, prefacing the shedding of the existing one.

For further reading on this topic the student is referred to 'Insect Hormones', by Sir Vincent B. Wigglesworth, in *Endeavour*, No. 91 (January, 1965).

In general, it is probable that a primitive endocrine system is in operation in the invertebrates as a whole. Investigation is rendered difficult by the fact that secretion of hormones is thought to be the province, in many cases, of small groups of cells, not organised into recognisable glands. In fact, it is not unreasonable to assume that the less the organisation of the nervous system, the greater is the dependence upon chemical co-ordination or, in other words, that the evolutionary

development of an endocrine system merely reaches its climax in the vertebrates and is not their exclusive province.

Plant Hormones

From the foregoing description of individual hormones in animals the general characteristics of these substances may be ascertained. It remains now to consider the secretion, distribution and function of comparable substances in plants. They may most profitably be studied in their relation to plant tropisms, since these reactions appear to be very largely controlled by hormones.

As a result of experimental work the normal course of phototropic response by a shoot or coleoptile is believed to be somewhat as follows. The hormone in question is (i) produced by the tip of the structure concerned, and (ii) is distributed backwards along the stem. (iii) It promotes elongation, and (iv) its distribution is retarded by light. The experimental evidence in favour of this mechanism may be considered for each phase individually.

(i) That the region of photoperception is not the same as the region of curvature has already been proved (page 458). If the tip of a coleoptile is removed there is no response to unilateral illumination, whereas if it is merely covered by a light-proof cap the curvature is indefinite, presumably due to the presence of a small quantity of hormone. If the tips of some coleoptiles are removed and placed on gelatin, and the gelatin is thereafter replaced on the decapitated coleoptile stumps, the latter exhibit the usual curvature when illuminated from one side only. This is explained on the assumption that the hormone produced by the tips passes into the gelatin.

(ii) Assuming that the hormone is produced at the tip it must be distributed backwards to the region of curvature, which may be some distance away. Further, if a mica plate be inserted into the plant on the side away from the light in a unilaterally illuminated plant no curvature occurs, presumably on account of the inability of the hormone to pass through this substance.

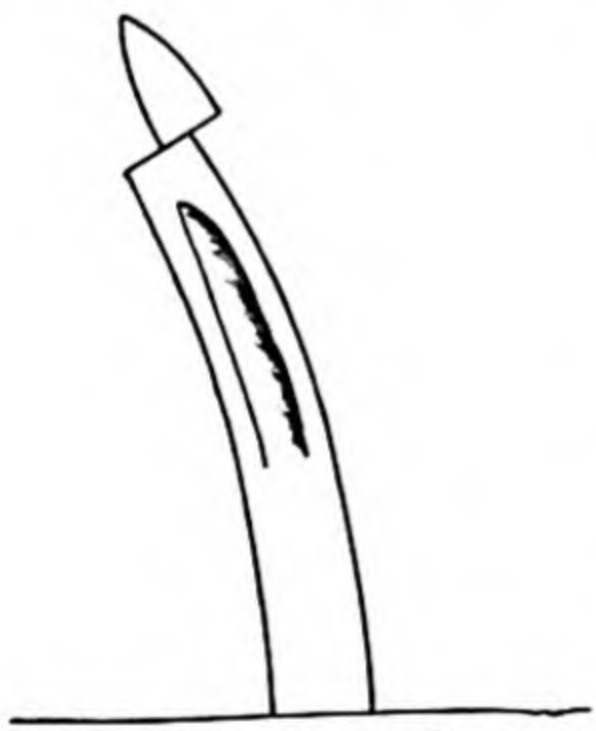


FIG. 287 – Experimental treatment of a coleoptile to show the effect of the hormone produced at the tip.

(iii) Elongation of the type which occurs in that region of a root or shoot where this phenomenon reaches its maximum is brought about by the enlargement of cells already formed, and not by further cell-division. If the tip of such a structure be removed this elongation ceases. That this is not merely due to the effect of the wound may be shown by the fact that immediate replacement of the tip results in normal

elongation. This is similarly the case if gelatin on which the tips have been resting for some time is replaced on the decapitated stumps. These facts can best be explained by the assumption of hormone-production by the tips. This hypothesis is further substantiated by a neat experiment. The tip of a coleoptile is removed and then replaced eccentrically on the uniformly illuminated stump. The stump then curves away from the side bearing the tip. This is apparently on account of the growth-promoting hormone, which reaches this side only, so that it elongates more rapidly than the other.

(iv) Taking the experimental evidence for the hormonic explanation of the previous phase of elongation as conclusive, it needs only to be recalled that elongation is most rapid in darkness to establish the fact that light must impede the action of the hormone. This it does apparently by delaying its distribution.

Thus when a shoot or coleoptile is subjected to unilateral illumination it results in a decrease in the rate of distribution of the growth-promoting hormone on the illuminated side. Thus the shaded side grows the more rapidly, with the result that the structure curves in the direction of the incident light.

Experimental research into the hormonic explanation of geotropic response has been confined principally to roots. Gravity is held responsible for the unequal distribution of a hormone produced in the tip, with a result that curvature occurs. But the hormone of the root tip is held to retard elongation, and not to promote it. This may be confirmed by an experiment similar to that described under (iii) above, when, on the removal of the tip, elongation is temporarily accelerated. If a root be placed in a horizontal position it has been proved that the hormone produced by the tip collects mainly in the lower half. This was done by fixing roots in a horizontal position so that they become geotropically stimulated. The tips were then removed and split longitudinally into upper and lower halves, after which they were placed on gelatin blocks. The tips of some roots growing in a vertical plane were now removed, and the gelatin blocks placed eccentrically upon the stumps. It was found by a majority result that the blocks which had borne the lower halves of the split tip caused the roots on which they were placed to bend towards them, whilst a similar result was obtained far less frequently from blocks which had carried upper halves. This indicates that more hormone was present in the lower halves of the horizontal roots than in the upper. Finally it may

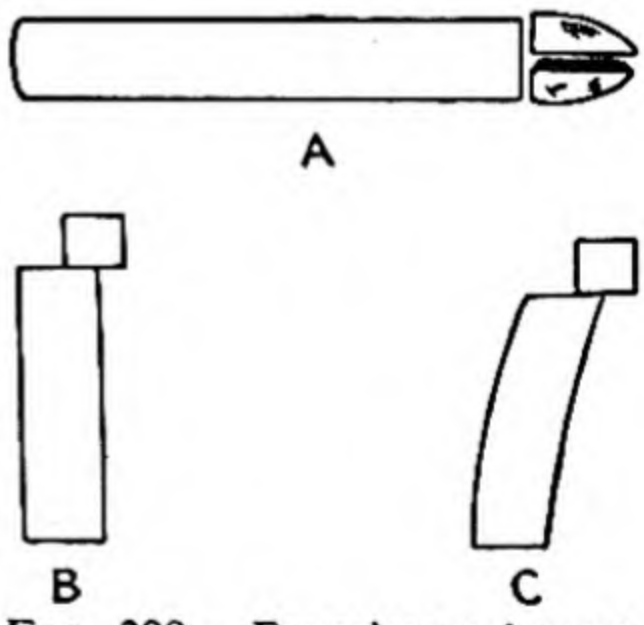


FIG. 288 – Experimental treatment of a root tip to show the localisation of hormone. For description see text.

be mentioned that if a root tip be removed and then replaced eccentrically on the stump, curvature takes place towards the side bearing the tip.

Thus when a root is exposed to unequal gravitational force – i.e. when it is not in a vertical plane – the growth-hormone elaborated by the tip becomes localised mainly on the lower side. This retards elongation, so that curvature occurs towards the vertical axis, since growth is more rapid on the upper side.

The identity, or at least striking similarity, of the hormones of the tip of a root and of a coleoptile is shown by the fact that coleoptile tips may be placed on gelatin, and this gelatin may be subsequently employed to stimulate curvature in a decapitated root-stump. The same hormone thus increases the growth-rate of stems and depresses that of roots.

It must be clearly borne in mind that hormones are equally effective in a natural environment: their functions are not exhibited merely in the artificiality of experimental conditions. Thus the hormone secreted in the tip of a shoot or a coleoptile is normally distributed backwards evenly to the region of elongation, thus stimulating uniform increase in length. That elongation is more rapid in darkness has already been shown by the use of the auxanometer (page 419), whilst retention in darkness for considerable periods results in the etiolation of stems and petioles. In this condition free distribution of the 'growth'-promoting hormone is allowed, whilst in ordinary solar illumination this is depressed, so that elongation is inhibited.

In the case of the young plumule, immediately after emergence from the testa, the distribution is apparently affected by gravity. It is to be assumed, as in the case of the root, that the hormone collects principally on the lower side, thus causing more rapid elongation on that side, so that the plumule is soon lying in a vertical plane and moving towards the surface of the soil.

The general effect of the root hormone in nature is to ensure that the root grows vertically downwards, though this path may to some extent be modified by the distribution of water in the soil. The mechanism of hydrotropism is not yet understood.

A rather different instance of response to a stimulus facilitated by the passage of a hormone is afforded by the so-called sensitive plant, *Mimosa pudica*, the leaves of which close together in a characteristic manner when they are touched. It has been shown by Snow (1925) and Ball (1927) that the hormone travels from the region of stimulation to other parts of the plant in the transpiration current, via the xylem, though on occasions it passes much more rapidly through the cells of the pith, in which case it can be conveyed either up or down the plant. This latter path is usually taken when the turgor of the cells is high and the water-tension in the xylem vessels low.

Auxins

In the foregoing description the general term 'hormone' has been applied to the various internally-elaborated substances responsible for the regulation of growth. It remains now to consider more of their specific nature. They have, in fact, been isolated, following extraction with chloroform, and are known to be present in all growing organs. The most significant ones are termed **auxins** and the importance of these phyto-hormones as correlators within the plant body is at once obvious. Nor do they always exist in active form, but in storage organs, for example, they are represented by inactive precursors – **auxinogens**. These are probably in the form of organic esters, the subsequent hydrolysis of which results in the liberation of free auxins. Three separate auxins have been isolated – *auxin a* ($C_{18}H_{32}O_5$ – ahydroxy-acid), *auxin b* ($C_{18}H_{30}O_4$ – a keto-acid) and *heterauxin* ($C_{10}H_9O_2N$ – β-indolylacetic acid), which has been synthesised. They have all been detected in human urine, indicating that they pass unchanged through the body, and they all appear to exert similar effects on plant organs, effects which are also produced by some synthetic products – e.g. phenylacetic acid.

The peculiarity of their distribution – almost entirely in a longitudinal direction and laterally hardly at all – indicates that something more than mere diffusion must be responsible.

In operation they appear to modify the plasticity of the cell-walls, in addition to which they may possibly act as co-enzymes in some oxidation systems. In the foregoing account the principal emphasis was laid on their significance in relation to plant tropisms, and it will be well here to note certain other processes for which they are now held to be responsible. Amongst these are the following:

(*a*) The failure of lateral buds to develop into leafy shoots when the terminal bud is present. It is believed that auxins from the latter exert an inhibitory effect upon the development of lateral buds.

(*b*) The formation of callus, galls and nodules is believed to be the result of meristematic activity initiated by the presence of auxins. In the case of galls and nodules the auxins may be liberated from the bodies of the insect larvae and bacteria respectively.

(*c*) Adventitious root formation is stimulated by the basipetal migration of auxins from developing buds to the pericycle of the cutting, there inducing meristematic activity.

(*d*) The development of fruits may be the result of the activation of auxins from receptacular and ovarian tissue under the influence of substances liberated from the pollen grains. The occurrence of *parthenocarpy* – the formation of fruits without actual fertilisation – makes it clear that the embryo plays no essential part. Fruit-formation has been induced by the application of auxin pastes to the tops of ovaries, pollination having been prevented.

(*e*) Auxins may well be responsible for the activities of meristems generally, including the cambium. The increase in activity of cambial tissue in the spring, with the consequent proliferation of additional xylem and phloem, coincides with a wave of auxin production by the developing young buds, and the two phenomena are undoubtedly correlated. Other factors may, however, be involved, since the artificial application of auxins to cambial tissues in winter does not induce a comparable increase in activity unless dormancy is first broken by, for example, treatment with ethylene.

(*f*) The inhibition of the formation of abscission layers may also be due to the influence of auxins set free by healthy leaves. It has been shown that petioles of de-laminated leaves are retained longer on the parent plant if smeared with heterauxin paste. The same principle applies to flowers. After pollination they produce greater quantities of auxin, and thus the developing fruit is more likely to be retained on the plant during its maturation: unpollinated flowers fall off more quickly. In the U.S.A. some varieties of apple tree, which were notorious 'droppers', have been sprayed with synthetic auxin, with very encouraging results.

(*g*) Reference has already been made to the phenomenon of photoperiodism (page 421), indicating a relationship between flower formation and length of daylight. It is believed that the production of flowers is due to hormone activity. It is possible that leaves, capable of day-length discrimination, may, at a certain optimum stage of day-night-periodicity, produce some hormonic substance which, passing to the growing-points, will induce a transition from vegetative branching to flower-production.

Gibberellins

In addition to the auxins, a further group of compounds, collectively termed the **gibberellins**, exert a regulating influence upon plant behaviour. Their existence first came to light as a result of investigation by the Japanese into Bakanae disease in rice, due to infestation by the fungus, *Gibberella*. Such plants grew more rapidly and ultimately became taller than healthy plants, prior to premature death. Gibberellin *A*, of formula $C_{22}H_{26}O_7$, was isolated in 1939 and is now one of a family of nine allied substances. Gibberellic acid – $C_{19}H_{22}O_6$ – was isolated in 1954 and exerts similar physiological effects.

The gibberellins are regarded as natural substances, accounting for the differences in height between related species of plant. Applied to dwarf forms in minute traces, they promote elongation, and when sprayed on their effects are quite startling. They have little influence when applied experimentally to taller varieties, although their natural presence in such has been demonstrated. Like prolonged cold treatment, they induce bolting in biennials. By stimulating cell elongation, gibberellins promote lengthening of internodes, whilst they are rapidly translocated both upwards and downwards.

From the reactions they induce it is apparent that they are different from auxins. Thus, whereas auxins inhibit leaf-fall and the formation of lateral branches, gibberellins do not: auxins retard root elongation and promote epinastic responses, but gibberellins do not. In many ways the effects of gibberellins, though not the same as those of auxins, are complementary to them. It has, therefore, been suggested that gibberellins are auxin activators, possibly because of their ability to inhibit auxin-destroying enzymes.

Kinins. It has been demonstrated experimentally that when explants, consisting of small portions of parenchyma (e.g. carrot, potato), are cultured, enlargement of cells is regular and rapid, whereas cell division is sporadic and appears to be induced by the presence of fragments of vascular tissue. A cell-division stimulant was found by Skoog to be present in a commercial preparation of nucleic acid, using tobacco pith as experimental material. This stimulant was isolated and identified as 6-amino-furfural-purine, subsequently termed *kinetin*. It is now known to be only one of a group of such substances, collectively termed *kinins*. Kinetin, and probably other kinins, is effective only by interaction with heterauxin (page 493) and it is probable that such substances are produced by degenerating cells, stimulating division of other cells. This may account, for example, for the rapid division of microspore mother-cells in anthers, following the disintegration of the tapetum.

Phytochrome. This pigment, of unknown composition, is the latest growth-regulator to be investigated. It occurs in two forms, one active and the other inactive. The active form is converted into the inactive by infra-red radiation, while the reverse change occurs on exposure to red light. The presence of such a substance may account for the failure of certain light-sensitive seeds to germinate in darkness, but to do so successfully in red light.

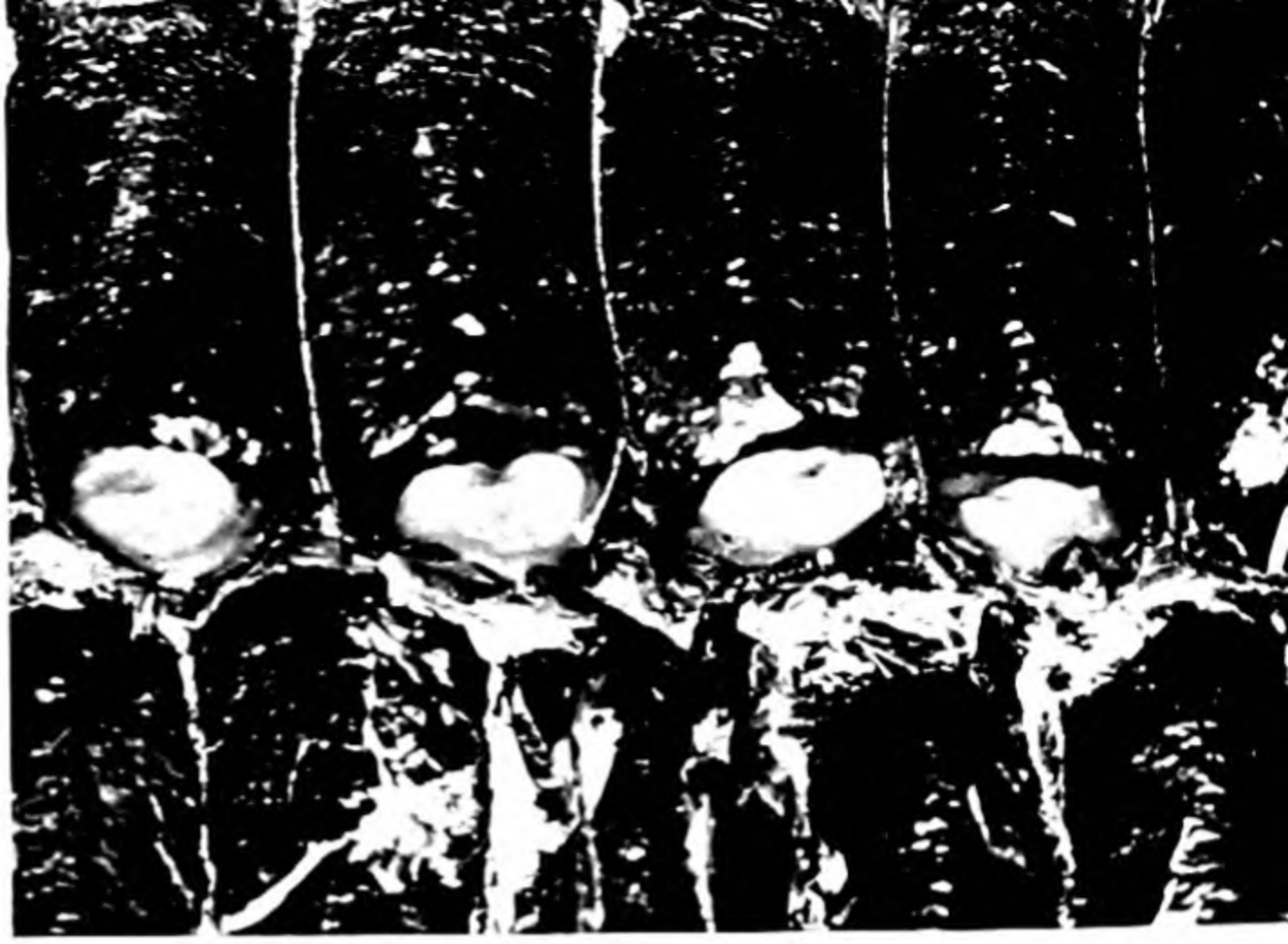
For red light to be effective a blue pigment must be present to absorb it. Such a pigment has recently been isolated, showing the necessary change in properties when exposed successively to red and infra-red rays. This pigment is now termed *phytochrome*.

It is also worthy of note that red light is effective in inducing flowering under short-day conditions in plants normally requiring longer daylight hours. It is possible that phytochrome is also involved here.

Thus, in both animals and plants, hormones afford a chemical mechanism for the conduction of impulses. In plants they are almost entirely responsible for the regulation of the organism by external conditions, whilst in animals this function is performed almost exclusively by the nervous system, a physical rather than chemical mechanism. The distribution of hormones in the animals is but very slightly controlled by external conditions. In spite of this, enough has been seen in the foregoing pages to demonstrate the essential similarity of these products of internal secretion in members of both animal and plant kingdoms.

Tubularia larynx (By courtesy of Dr Douglas P. Wilson)

Opelet or Snake-locks Anemone, *Anemonia sulcata* (By courtesy of Dr Douglas P. Wilson)



Young worker larvae in cells. (By courtesy of Dr C. G. Butler and Messrs Flatters & Garnett Ltd.)

Tadpole, showing the operculum. (By courtesy of the executors of the late Alan Dale and of Messrs Flatters & Garnett Ltd.)

The birth of a Mosquito. (By courtesy of the U.K. Committee for the World Health Organisation of the U.N.)

PART V

Development and Reproduction

So far the form and function of adult animals and plants have been considered in some detail. In Part III the relationship between component cells and individual organisms was discussed. Whatever the conclusions arrived at, it has to be borne in mind that the vast majority of animals and plants owe their existence to the repeated division of a fertilised egg and the subsequent differentiation of the products. Such constitutes their development, the study of which is termed **embryology**. Accordingly three representative Chordata are considered, and special attention should be paid to cleavage and the formation of germ-layers in *Branchiostoma*, since these processes are here so typically represented. Finally an outline of the development of the rabbit is given.

In higher plants the prelude to fertilisation is pollination. Both these processes have already been described in Chapter 16, together with an account of the formation of seeds and fruits and the early development of the plant embryo. Here it remains to consider the subsequent process of germination, often separated from the liberation of the seed by a considerable period of time.

In conclusion, the life-histories, typical and modified, of animals and plants are discussed, so that some idea may be acquired of the processes involved in the perpetuation of the race. The origin of sex is considered, whilst an attempt is made to show the fundamental distinction between reproduction, as effected by fission, and the fusion of cells (syngamy) in so-called sexual reproduction. Processes accompanying syngamy have become secondarily modified to result in increase in numbers – i.e. reproduction – but primitively the fusion of two cells can result in nothing but decrease in numbers.

CHAPTER 28

Embryology of Branchiostoma

Embryology involves a study of the events whereby an egg develops into an adult animal. In the vast majority of cases this process is prefaced by the fertilisation of an egg by a spermatozoön. The principal features of this phenomenon will be indicated before proceeding to a study of the development of selected chordates.

Fertilisation

This may be defined as the union of an egg with a spermatozoön, the nucleus of both these cells containing only the haploid number of chromosomes, to form a fertilised egg, the nucleus of which contains the diploid number of chromosomes. It has been studied in a number of animals, but most knowledge has been acquired from an investigation of the process in marine invertebrates, especially the echinoderms (starfish and sea urchins). If mature sea urchin eggs are placed in a Petri dish of sea water and sperms are spread over them it is observed, by microscopic examination, that each egg is quickly surrounded by a number of active sperms and may rotate rapidly like a 'Catherine wheel'. Before fertilisation the eggs are covered each with a layer of jelly, beneath which lies a thin *vitelline membrane*. It has been demonstrated that the eggs secrete *fertilisin*, an enzyme which activates the sperms, causes them to adhere to the surface of the eggs and facilitates penetration. That this is so is demonstrated by the fact that fertilisation does not occur if the eggs are previously thoroughly washed in sea water. At the point where the sperm touches the egg a *fertilisation cone* of cytoplasm appears, only to retract later and pull in the head and middle piece (page 349) of the sperm, the tail being abandoned. In most animals the tail does, in fact, penetrate the egg. Progressively from the point of entry the vitelline membrane begins to harden to form the *fertilisation membrane*, possibly to preclude the entry of further sperms. Inside the egg the cytoplasm shrinks away from the membrane, from which it becomes separated by a *perivitelline fluid*. In most animals only one sperm penetrates an egg, but in birds several are drawn in, though only one fuses with the nucleus of the egg. Penetration, although usually rapid, may last up to an hour.

The egg is not necessarily mature when the sperm enters. For example, in some vertebrates the egg is liberated at the secondary oöcyte stage (page 320). If a sperm penetrates such an egg the former remains inactive until the latter has completed its second meiotic division. During pene-

tration the head of the sperm and the region immediately posterior to it, carrying the centrosome, rotate through 180°, so that the sperm advances towards the egg centrosome first. A spindle is developed in association with the released centrosome and upon this the paternal and maternal chromosomes become disposed. Without further delay they complete the first mitotic division, giving rise to the first two nuclei of the embryo. In fact, any sort of resting stage after fertilisation is very much the exception amongst animals. Thus the diploid number of chromosomes is restored in the nucleus of the zygote.

Peculiarities of fertilisation are indicated individually for the succeeding types whose development is subsequently described, starting with *Branchiostoma*.

When fertilisation occurs in this animal the egg has reached only the stage of a secondary oöcyte (page 320). It is covered by a vitelline membrane, within which is a layer of yolkless cytoplasm, containing many mitochondria (page 303). There is an area of yolky cytoplasm nearer the

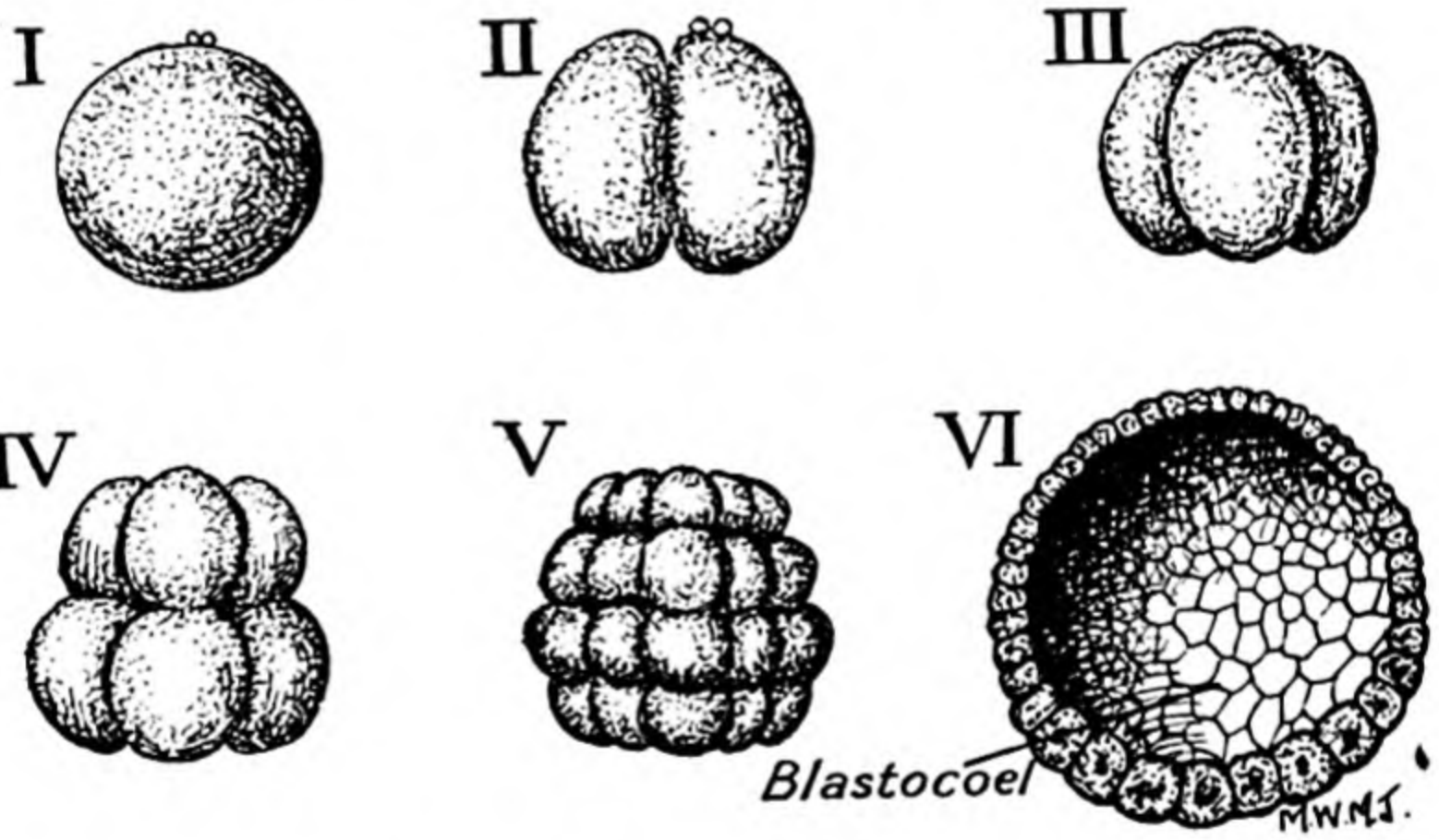


FIG. 289 – *Branchiostoma*. Cleavage of the egg to the blastula stage.

so-called vegetative pole, whilst nearer the animal pole lies the nucleus. As the total amount of yolk is relatively small the egg is described as *microlecithal*.

The fertilising sperm enters towards the vegetative pole and maturation is completed, the second polar body now being extruded. This is followed by the rearrangement of the cytoplasmic areas. The superficial layer of granular cytoplasm streams to the posterior end (vegetative pole) and becomes a well-defined crescentic area. Meanwhile a layer of clear cytoplasm appears at the periphery of the egg. These regions of the egg which are differentiated in this way will, during development, give rise to specific

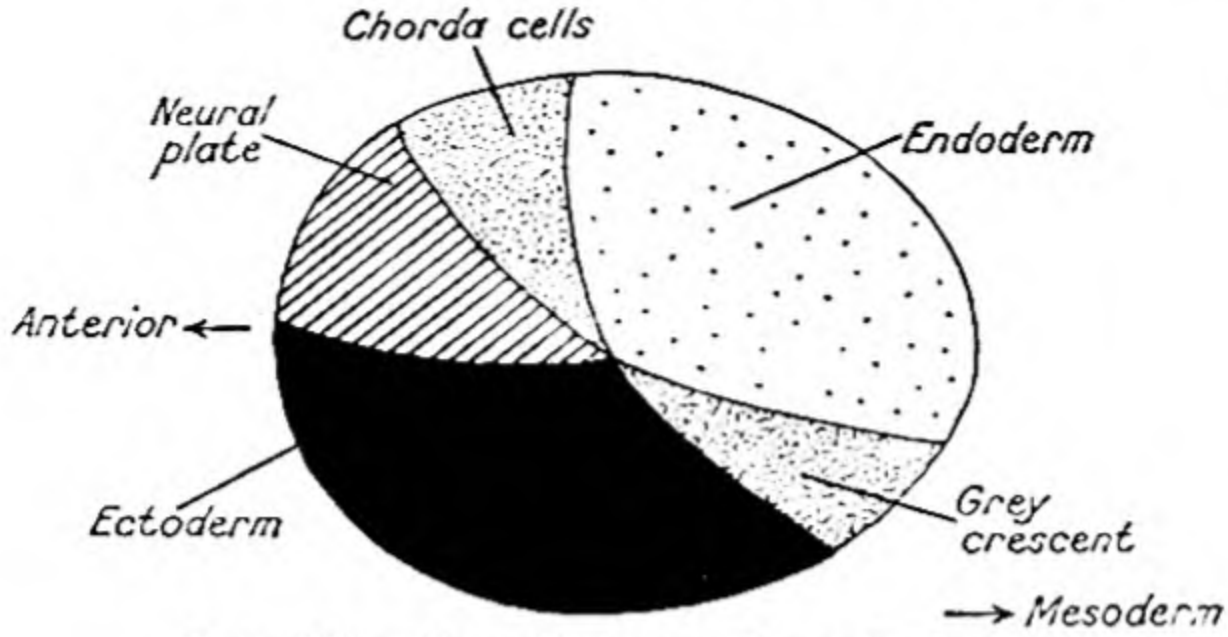


FIG. 290 – *Branchiostoma*. Lateral view of early embryo, showing presumptive areas.

organs. Because of the formation of this pattern which predetermines future development, the egg is described as a *mosaic*.

Cleavage

Since the amount of yolk is small, cytoplasmic cleavage can keep pace with nuclear division; such cleavage is described as total, or *holoblastic*. The planes of cleavage bear a definite relationship to the mosaic pattern of the egg, and thus the areas become distributed very specifically. The products are thus predetermined in respect of the parts of the embryo to which they will give rise; such cleavage is described as *determinate*. Thus, in general terms, it may be stated that the clear cytoplasm gives rise to ectoderm, the yolky cytoplasm to endoderm and the crescent of granular cytoplasm to mesoderm. The first cleavage furrow passes through both poles and bisects the mesodermal crescent, thus forming two blastomeres representing right and left halves of the future embryo. The next furrow is at right angles to the first in a vertical plane. The third is horizontal but above the equator of the embryo, so that the anterior blastomeres (*micromeres*) are smaller than the posterior's. Meridional divisions follow, succeeded by a further horizontal cleavage in each half, so that sixty-four blastomeres are now present. Further irregular cleavage results in the formation of a **blastula**, whose cavity is the **blastocoel**.

Gastrulation

This commences about four hours after fertilisation. The vegetative pole becomes flattened because the megameres divide less rapidly than do the micromeres. In this way a triangular *endodermal plate* is formed, to the sides and posterior end of which is the *grey crescent*. Rather smaller cells lie adjacent to the plate. These are the *chorda cells*, destined to give rise to the notochord. The *neural plate* lies in front of the chorda cells and from it the central nervous system is eventually derived. The endodermal plate becomes concave and bulges into the cavity of the blastula,

which is thus obliterated. This invagination takes place more rapidly on one side and the region overhanging this point is known as the *dorsal lip*. Here cell migration occurs rapidly and cells pass over the lip towards the future posterior end. This process of overgrowth is known as *epiboly*. It proceeds round the edge of the invagination (sometimes referred to as the *germ ring*), the embryo becoming elongated antero-posteriorly. As a result of invagination the centre of gravity moves, causing the embryo to rotate through an angle of 90°. Eventually the blastocoel becomes completely obliterated and the embryo is now referred to as a **gastrula**. Its cavity, termed the **archenteron**, opens to the exterior by the **blastopore**, itself marking the future posterior end of the body. Lining the archenteron are the inturned cells from the crescent, whilst the roof (i.e. the dorsal side) is a strip of inturned chorda cells. The floor is composed of yolky cells, derived from the vegetative hemisphere of the original blastula. Together these cells constitute the **hypoblast**. Gastrulation is completed in about eight hours. The external cells of the embryo constitute the **epiblast** and become ciliated. The dorsal side of the embryo becomes flattened, whilst as elongation takes place the blastopore becomes steadily smaller. Ciliary activity results in rotation of the embryo, which, some three or four hours later, is liberated as a free-swimming larva. This independent existence is essential, since the small supply of yolk is soon exhausted. The hypoblast and epiblast are known as **germ-layers**, for all the organs of the future adult are derived from them. There is formed at a later stage a third layer, known as the **mesoderm**, between the hypoblast and epiblast. Though also described as a germ-layer it is in reality developed from the hypoblast. Following the separation of the mesoderm and the origin of the notochord, the epiblast is known as the **ectoderm** and the hypoblast as **endoderm**.

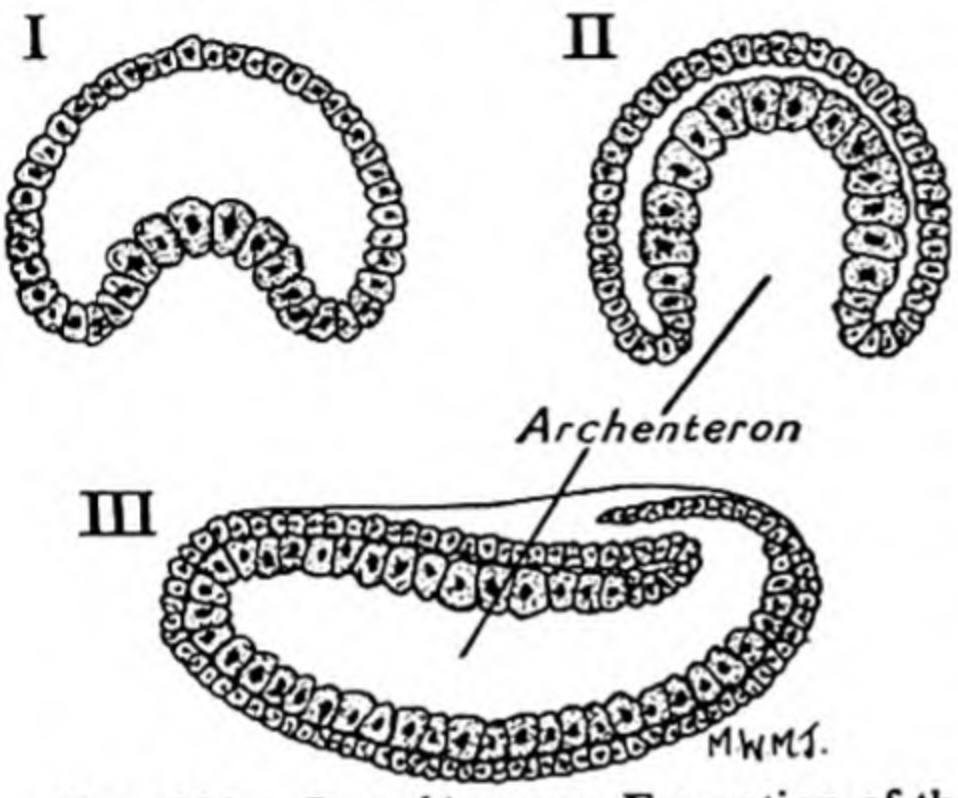


FIG. 291 – *Branchiostoma*. Formation of the gastrula.

Formation of Nerve-cord

The nerve-cord arises from the ectoderm. A layer of cells along its dorsal surface becomes flattened to form the **neural plate**. It sinks in somewhat along the middle line and a **neural fold** arises on either side. The two folds eventually meet and coalesce dorsally, whilst the structure so formed, at first solid, later becomes tubular, lying just beneath the

ectoderm. This is the nerve-cord. It is only at the extreme anterior end that the two neural folds do not immediately meet, so that in this region an aperture is temporarily left, the **neuropore**, represented in the adult by

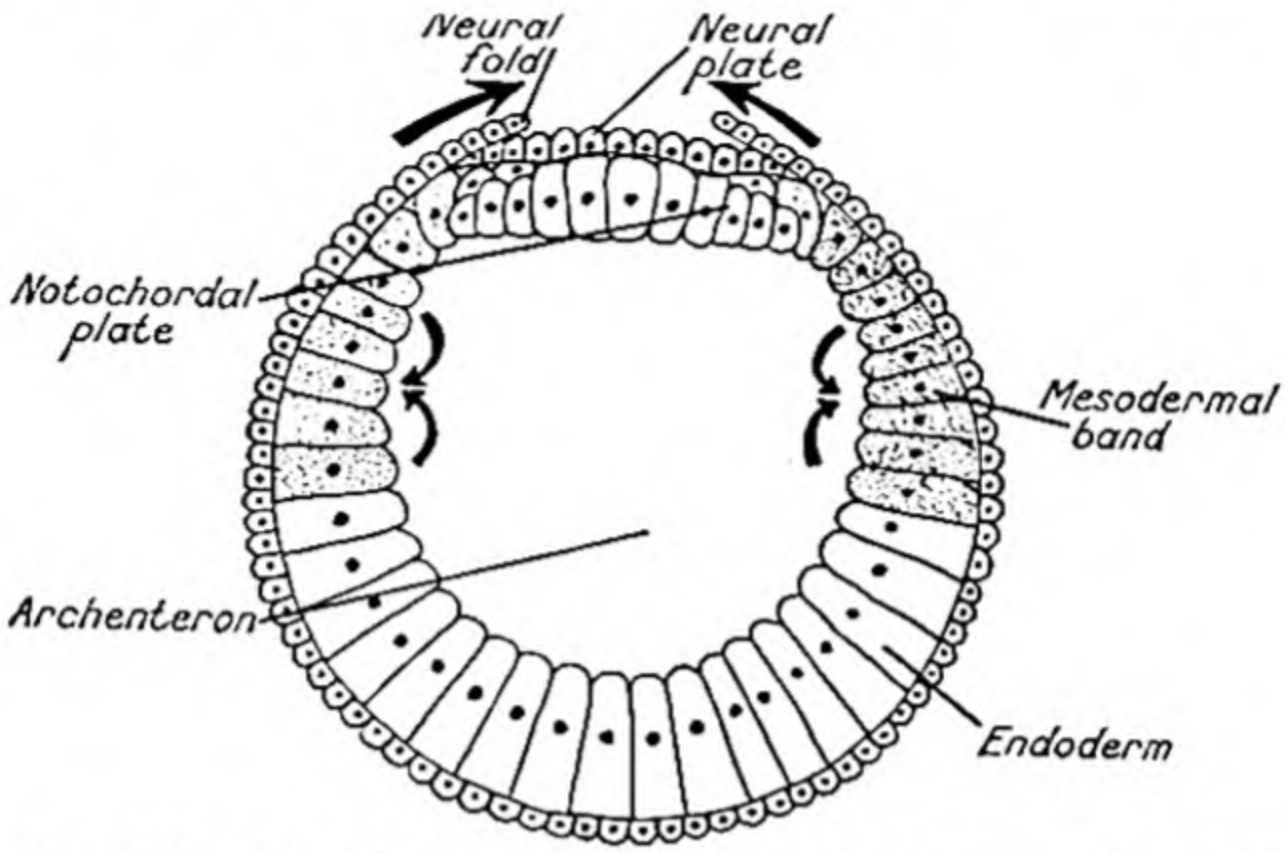


FIG. 292 – *Branchiostoma.* Transverse section of completed gastrula, showing early stages in development of nerve-cord, notochord and mesoderm.

Kölliker's pit. At the posterior end, on the other hand, the neural folds come to roof over the blastopore, which now communicates only with the cavity of the nerve-cord and not with the exterior. This opening between the blastopore and nerve-cord is the **neurenteric canal.**

Formation of Notochord

Along the mid-dorsal line of the roof of the archenteron lies the

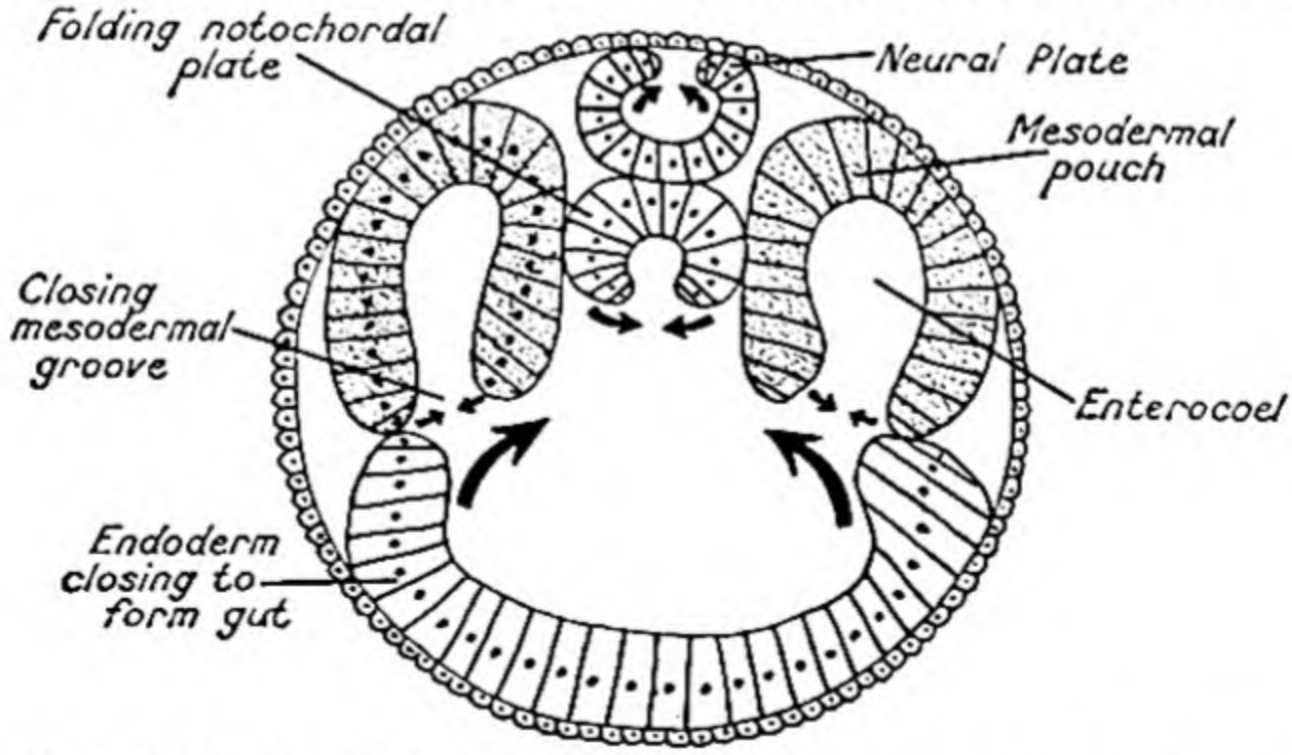


FIG. 293 – *Branchiostoma.* Transverse section, showing later stages in development of nerve-cord, notochord and mesoderm.

strip of chorda cells, constituting the *notochordal plate*. The edges of this plate bend down ventrally, like an inverted gutter, and eventually meet to form a solid rod – the **notochord**. The cells of this rod become vacuolated, whilst later the whole becomes enclosed within a fibrous sheath. The notochord functions as the main axial skeleton of the animal and is one of the most important characteristics of all Chordata.

Formation of Mesoderm

The mesoderm is formed by separation from a portion of the hypoblast on either side of that giving rise to the notochord. Each of the bands of tissue concerned arches over, with the groove so formed directed downwards and thus communicating with the archenteron. At this point a transverse partition arises, cutting off a small, anterior portion from the remainder of each fold posteriorly. The bases of these anterior folds now become completely closed, so that in this way a pair of somites is

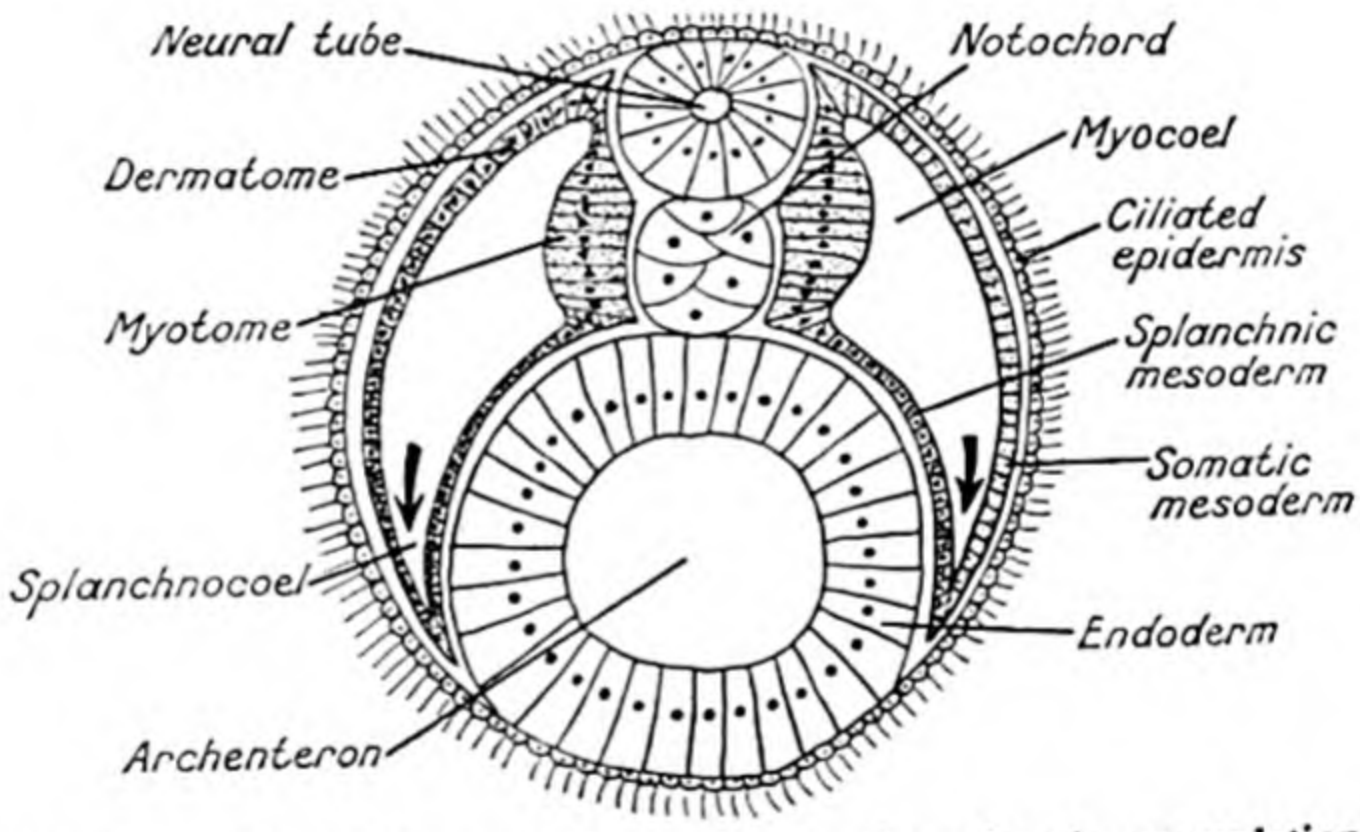


FIG. 294 – *Branchiostoma*. Transverse section, showing completion of formation of nerve-cord, notochord and gut, with the ventral extension of the mesoderm.

formed, cut off from the cavity of the mesodermal folds posteriorly. Eventually the remainder of each fold becomes completely closed off from the archenteron, progressively from in front backwards, and following this separation the tube thus formed on each side becomes divided up into somites by the laying down of transverse partitions. This is in contrast to the first pair of somites, which became demarcated from the remainder of the mesoderm before separation from the archenteron was completed. At the time of liberation of the larva only two pairs of somites are present.

The mesodermal somites now commence to extend ventrally, running between the gut-wall and the ectoderm. Eventually each meets the corre-

sponding structure from the other side in the mid-ventral line, and their separating walls disappear. Thus each pair of somites forms a hoop of hollow mesoderm extending ventrally beneath the archenteron. The cavity between the two layers of mesoderm is the **coelom**, whilst the mesodermal walls of the cavity constitute the coelomic epithelium. The epithelium lying against the endoderm is known as the splanchnic layer, or **splanchnopleur**, whilst that against the ectoderm is the somatic layer, or **somatopleur**. The original pouches – i.e. the mesoderm formed prior to their ventral extension around the gut – become further differentiated. Their cavities are known as **myocoels** and become separated from the cavities (**splanchnocoels**) of the ventral parts by partitions. The inner wall of each myocoel, lying alongside the nerve-cord and notochord, becomes much thickened to form a muscle-block, or **myomere**, whereas its outer wall becomes the **cutis**. The myocoels retain their segmental arrangement, but the septa between the splanchnocoels break down so that ventrally a continuous perivisceral coelom is formed, enclosing the gut throughout its entire length. The myomeres, at first regular, soon become V-shaped, and alternate on right and left sides.

As well as the mesodermal cavities already described, there arises from the anterior end of the endoderm a pair of **head-cavities**, peculiar on account of their asymmetry. Though of symmetrical origin, the right one soon becomes very much enlarged, whilst the left one establishes a communication with the base of an ectodermal inpushing, known as the **preoral pit**, and there opens to the exterior. In the adult this is represented by **Hatschek's pit**.

Only one other feature in connexion with the development of mesoderm is important, and that is the formation of the gonads. In each of segment 25 to 51 a downgrowth into each myocoel gives rise to a **gonocoel**, thus forming the cavities of the gonads, their walls becoming the germinal epithelium. The body-wall in the region of the gonads become distended and later bursts, so that the genital products are shed into the atrium (page 506). The sexes are separate.

Alimentary Canal

The mouth is perforated at the anterior end of the body and to the left of the middle line. It becomes ciliated. The neurenteric canal now becomes closed, and the anus is perforated just beneath it. Meanwhile the splanchnopleur is becoming modified to form a coat of involuntary muscle surrounding the gut, and a liver diverticulum pushes forwards from the right side of the gut.

The development of the pharyngeal region is so highly specialised and of so little relevance to that of higher forms that it will not be considered in detail here. Suffice it to say that to the right of the mid-ventral line arise two rows of gill-slits, the more dorsal row, about eight in number, being described as secondary and the ventral set, in which there are some

twelve slits, as primary, since they arise before the secondaries.

Whilst still occupying this curious position the two sets of gill-slits become separated by a rudimentary **endostyle.** This originates in the lining of the pharynx in front of the most anterior gill-slits and then extends backwards between the primary and secondary gill-slits. As it elongates it assumes the form of a shallow groove, lined by cells, some of which are ciliated, whilst others secrete a mucous substance. In this form it assists in the adult in the manipulation of food. It represents the thyroid gland of higher forms.

At this point a more reasonable symmetry is developed, for the two lots of gill-slits and the endostyle start to move in a ventral direction. This movement stops only when the endostyle is in the mid-ventral line and the primary gill-slits on the left side more or less correspond in position to that of the secondary on the right. At the same time the mouth becomes reduced in size and it original margin is drawn in on all sides to form the **velum**. This simplicity of arrangement of the gill-slits does not persist for long, for subdivision takes place by the downgrowth of **tongue-bars** from the roofs of the original slits. Thus these tongue-bars do not contain any coelomic cavity, for they are formed by the subdivision of structures which pass through the coelom but are not part of it.

Atrium

The gill-slits of *Branchiostoma* do not open direct to the exterior but into a portion of the outside world, enclosed between the body-wall and a fold of skin – the **atrium**. This latter arises in the form of a pair of

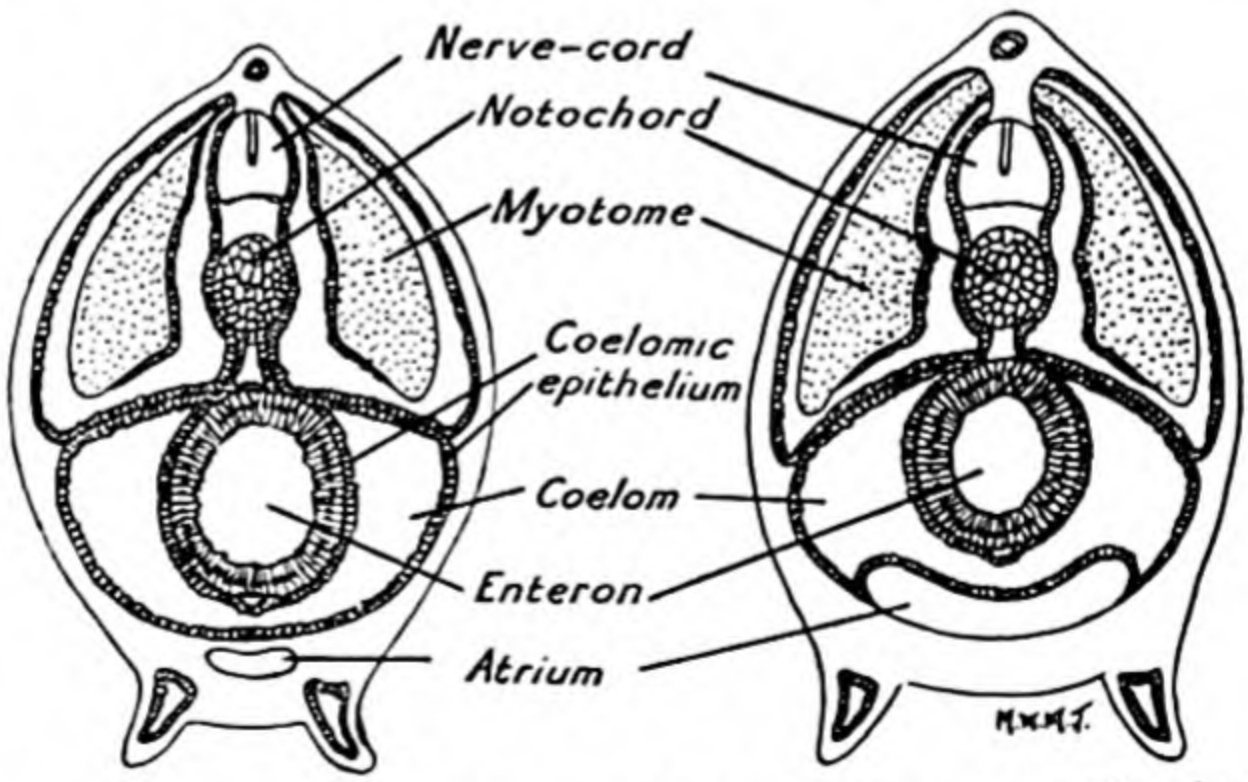


FIG. 295 – *Branchiostoma*. Diagrams to show enlargement of atrium. Transverse sections.

longitudinal folds, known as **metapleurs,** one above the gill-slits on either side. Each fold grows in a ventral direction, and from it there arises a

shelf, known as an **epipleur**, growing in towards the mid-ventral line, where it meets and fuses with the corresponding structure of the other side, thus enclosing a space. At the posterior end the atrium is in communication with the exterior by a small **atriopore**.

Nephridia

The excretory organs of *Branchiostoma* arise as small, blind, ectodermal outpushings at the top of the original gill-slits, prior to the formation of tongue-bars. Each extends for some distance down the coelomic cavities of a primary gill-bar and opens to the exterior near the apex of the neighbouring tongue-bar. Flame-cells are developed as outgrowths from the tube. Hatschek's nephridium arises similarly as a small tube near the preoral pit, but instead of leading to the exterior it communicates with the pharynx of the adult.

The following table affords a summary of the various structures found in *Branchiostoma*, and indicates the germ-layer from which each is derived:

ORIGIN OF STRUCTURE IN BRANCHIOSTOMA

Ectoderm	Mesoderm	Endoderm
Epidermis	Dermis	Lining of alimentary canal
Lining of atrium	Myotomes	Liver
Nephridia	Blood-vessels	Endostyle
Wheel organ	Lining of coelom	Inner part of gill-bars
Outer part of gill-bars	Gonads	
Nerve-cord	Connective tissue	

PRACTICAL WORK

Examine and draw prepared slides of various stages in the development of *Branchiostoma*.

Examine and draw a transverse section of an adult in the pharyngeal region, so that the final result of the process of development may be the better understood, as well as the means of attaining it.

CHAPTER 29

Embryology of Rana

The Egg and Fertilisation

The first reduction division occurs as soon as the egg is liberated from the ovary, the polar body being retained within the vitelline membrane. Each egg, measuring about 1.7 mm. in diameter, is clearly divided into two hemispheres. The animal hemisphere is composed of clear cytoplasm and is covered superficially by a layer of dark brown pigment (*melanin*), extending just below the equator. The vegetative hemisphere is whitish in colour and contains numerous yolky granules. With this concentration of yolk in one pole the egg is described as *medialecithal.* As the egg passes down the oviduct the wall of the latter secrets a layer of jelly-like material about it. Mating occurs in spring, a male mounting the back of a female and maintaining its position by means of its thumb pads. As the eggs are laid the male sheds seminal fluid over them. The fertilising sperm enters the egg about 40° from the animal pole, the tail remaining at the surface. The sperm path is marked by a trail of pigment drawn in from the exterior. At this point the vitelline membrane is raised and a perivitelline space appears. The egg is now free to rotate within its membrane and takes up a position with the heavier vegetative pole directed downwards. Meiosis is now completed and the male and female nuclei (often termed *pronuclei*) fuse to restore the diploid number of chromosomes (26). Contact with water causes the jelly-like material to swell, forming the characteristic spawn. On the side of the egg diametrically opposite the point of entry of the sperm the superficial pigment flows inwards to form an area where the melanin is more dispersed. This is the *grey crescent* and lies in the pigmented animal hemisphere. When established, the grey crescent gives to the fertilised egg a bilateral symmetry, marking, as it does, the future dorsal side of this embryo.

Cleavage

The first cleavage furrow is vertical and bisects the grey crescent symmetrically. The second likewise is vertical and at right angles to the first, whilst the third is horizontal but above the equator, dividing the embryo into an upper animal hemisphere, composed of four small blastomeres (*micromeres*), and a lower vegetative hemisphere, consisting of four larger *megameres.* As cleavage continues, division is more rapid in the animal hemisphere than in the vegetative, where it is impeded by yolk. Ultimately a **blastula** is formed, the roof and sides consisting of

small, pigmented cells and the floor of larger, yolky cells. By vital dye staining (see below) it has been made possible at this stage to map out

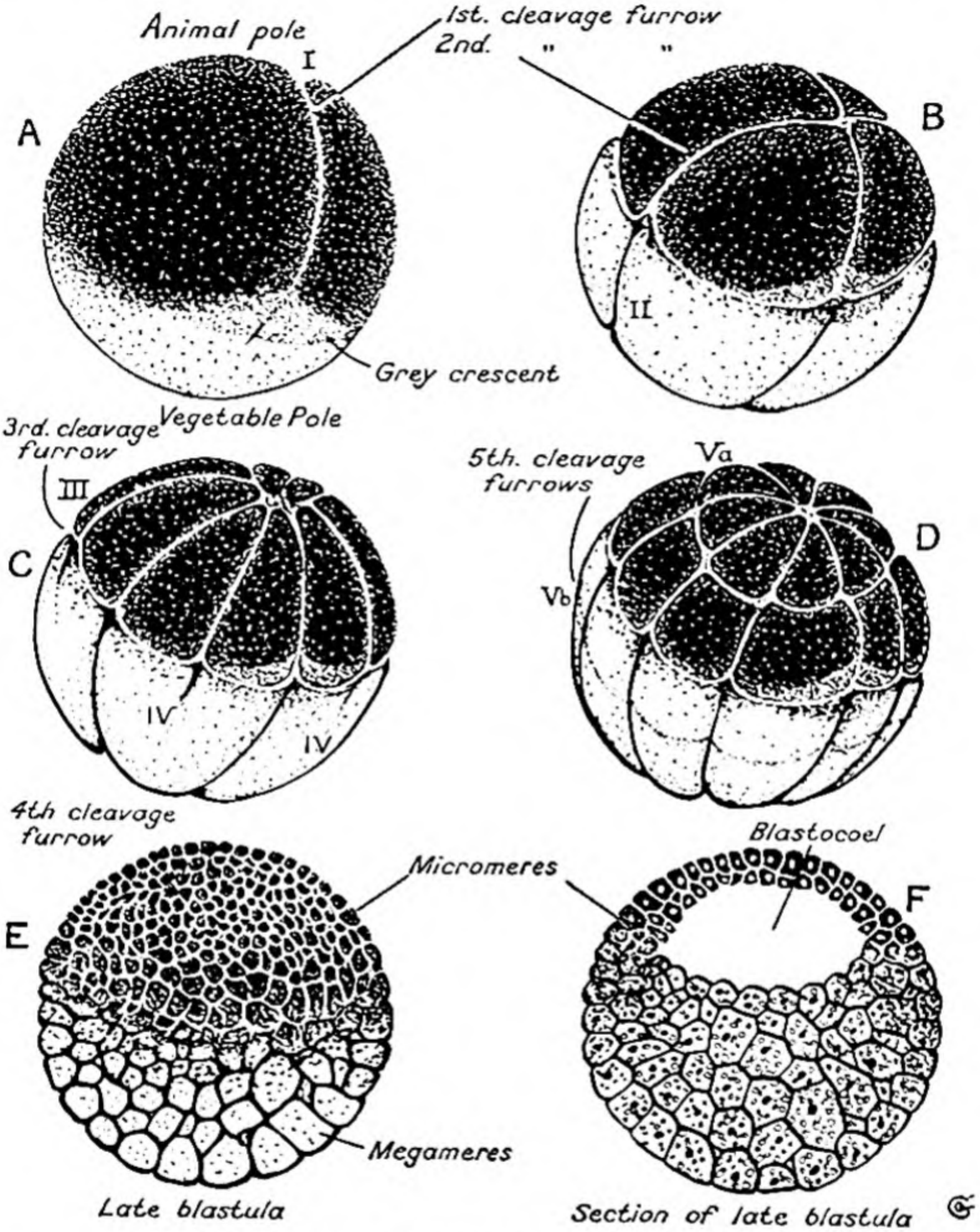


FIG. 296 – *Rana*. Cleavage of zygote to form blastula.
A., First cleavage vertical; *B*., Second cleavage vertical; *C*., Third cleavage horizontal, fourth cleavage vertical; *D*., Fifth cleavage vertical; *E*., Late blastula – external view; *F*., Late blastula – vertical section. Note also the tangential divisions.

the fates of the various parts (presumptive areas) of the blastula. These are indicated in Fig. 298.

Gastrulation and Mesoderm Formation

Owing to the presence of a considerable quantity of yolk the process of gastrulation is somewhat modified from the simple course it takes in *Branchiostoma*. The study of gastrulation has been very largely facilitated

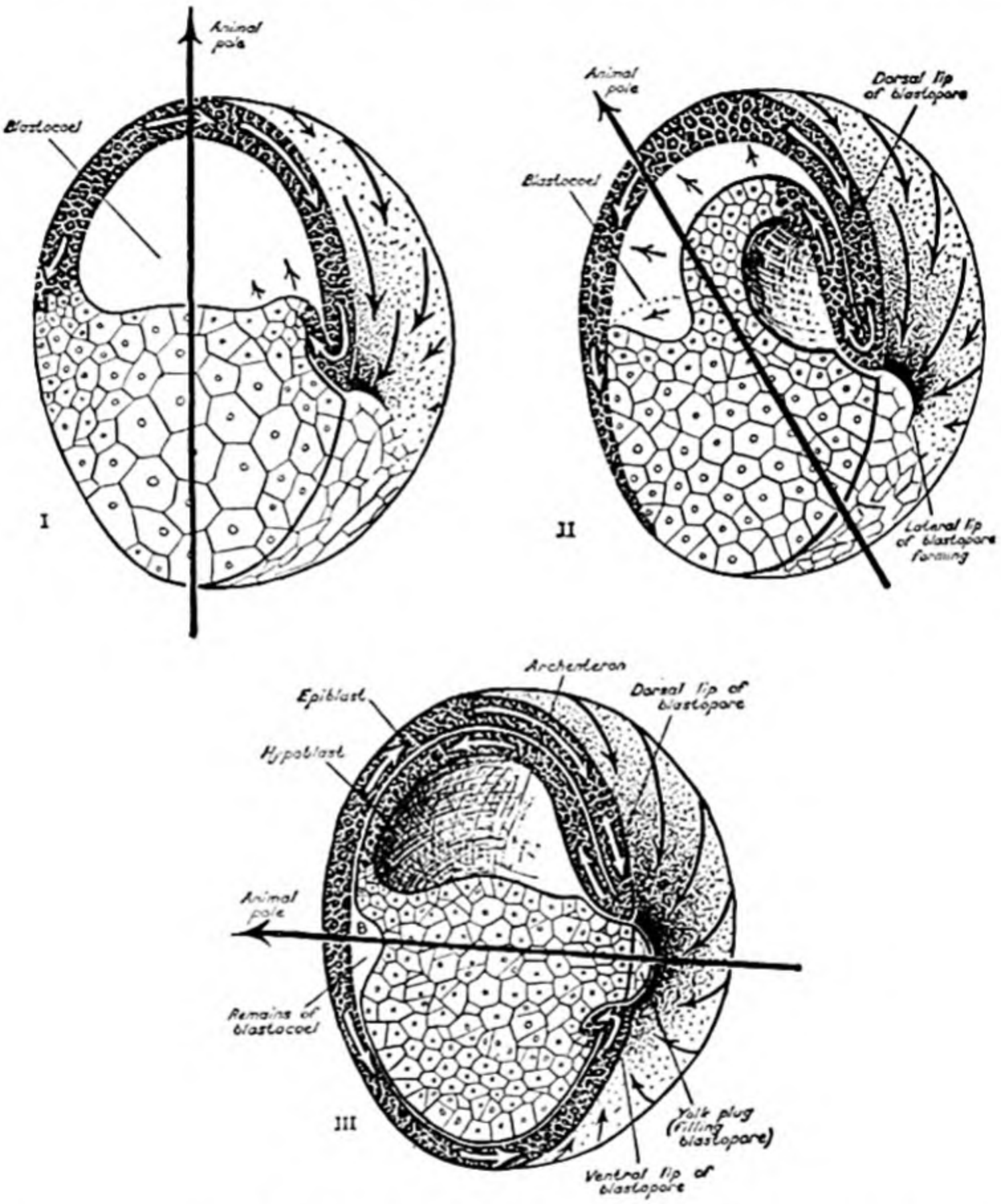


FIG. 297 – *Rana*. Stages in gastrulation.
I., Initiation of the dorsal lip of the blastopore; II, Lateral extension of the lip of the blastopore – the blastocoel is becoming reduced and the archenteron appearing; III, The completed gastrula.

by a technique involving staining of tissues without destroying them or impairing the health of the developing embryo, a method elaborated by Professor Vogt, of Zurich. This vital dye staining involves the placing of the embryos for a few minutes in contact with small blocks of gelatin

containing a suitable dye. The cells of the organism in contact with the block absorb the dye, and thereafter their movement and ultimate fate may be watched. By such means the details of gastrulation have been worked out. The **blastopore** first appears as a crescentic groove to one side of the embryo, in the area of the grey crescent, and this marks the position of the dorsal lip. It becomes extended downwards on either side to form the lateral lips, whilst eventually the pore is completely surrounded as a result of the fusion of these lips beneath. A plug of yolk cells remains visible through the blastopore. During this time vital dye staining has demonstrated the fact that the tissues around the blastopore converge upon it and eventually pass within it. They move up towards the region of the neural plate (see below) and there become aggregated to form the roof of a new gut-cavity, or **archenteron**, the floor and side-walls of which are constituted by yolk-cells. The remainder of the cells passing through the blastopore go to form the **mesoderm**. The archenteron enlarges and presently becomes the principal space in the embryo. In consequence there is a shift of the centre of gravity of the embryo and the whole gastrula suddenly rotates through 100° within its membrane, with the result that the blastopore now comes to lie at the posterior end of the embryo, with the future dorsal surface uppermost. The roof of the archenteron and its lateral extensions are the only portions of the hypoblast which arise as a result of the process of migration of tissue over the rim of the blastopore (Fig. 297).

Notochord

A rod of cells along the dorsal side of the hypoblast marks the position of the future notochord, which is formed as a result of the complete separation of this rod from the roof of the archenteron. This separation is effected distinctly only anteriorly, whilst posteriorly the layers are less clearly demarcated, this culminating at the dorsal lip of the blastopore, where all three germ-layers are continuous.

Nerve-cord

Eventually the blastopore is reduced to a slit and closure proceeds from the dorsal lip towards the ventral lip, the lateral lips steadily being drawn together as if being closed by a 'zip' fastener. After closure the slit lies along the antero-posterior axis and anterior to it there appears, on the dorsal surface, a flattened area, shaped like a much elongated figure 8: this is the **neural plate**. Soon the edges, constituting the **neural folds**, become raised and the centre depressed to form the **neural groove**. The folds rise up and bend inwards to enclose the neural plate (Fig. 299), forming the **neural tube**. The neural folds are more widely separated at the anterior end where, by their fusion, the brain is formed. The embryo at this stage is referred to as a **neurula**. The neural tube remains open at the anterior end via the **neuropore**, but this becomes constricted as the

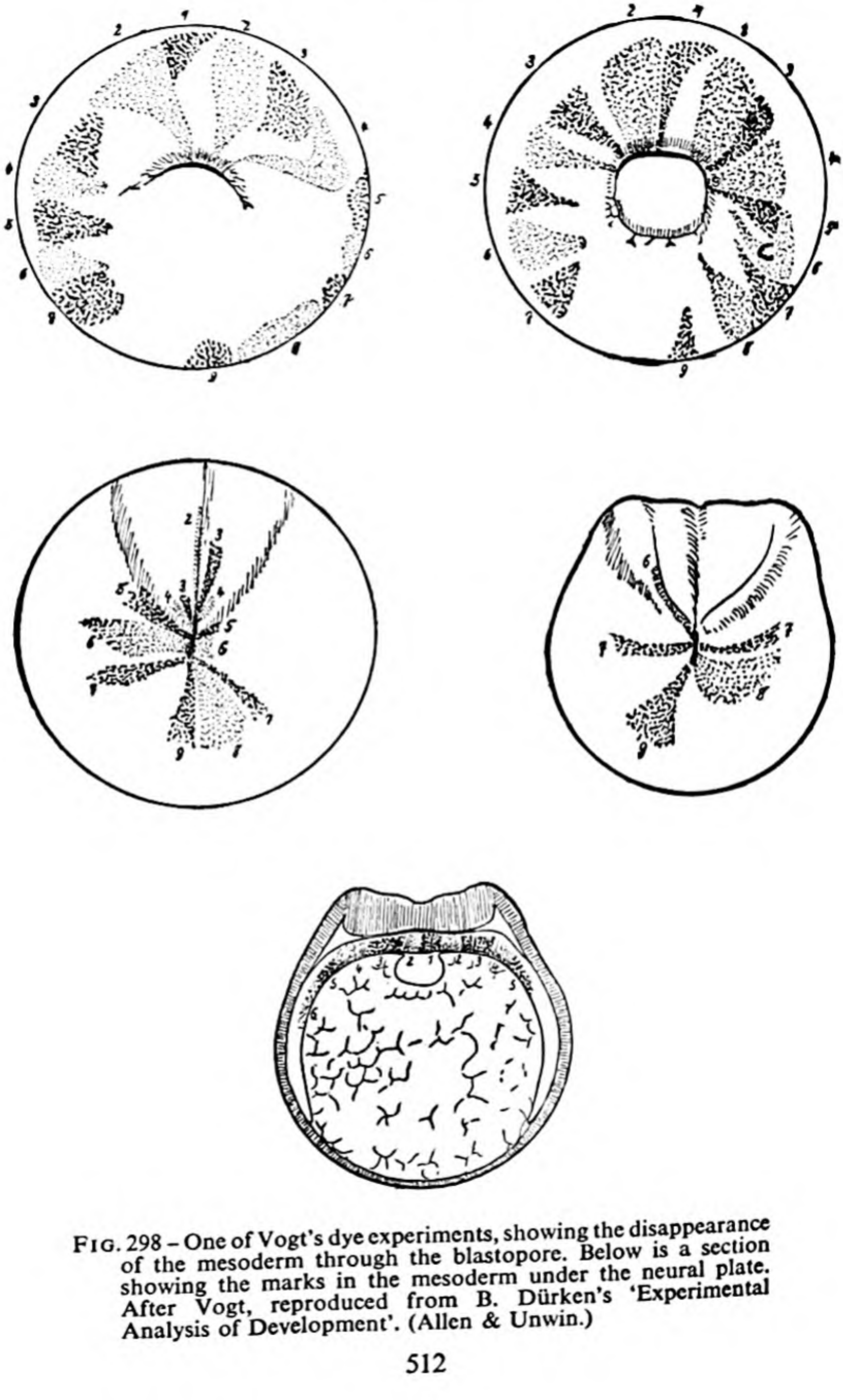


FIG. 298 – One of Vogt's dye experiments, showing the disappearance of the mesoderm through the blastopore. Below is a section showing the marks in the mesoderm under the neural plate. After Vogt, reproduced from B. Dürken's 'Experimental Analysis of Development'. (Allen & Unwin.)

development of the brain proceeds. Posteriorly the neural tube communicates for some time with the archenteron through the **neurenteric canal**, which subsequently closes. But the whole neural plate is not con-

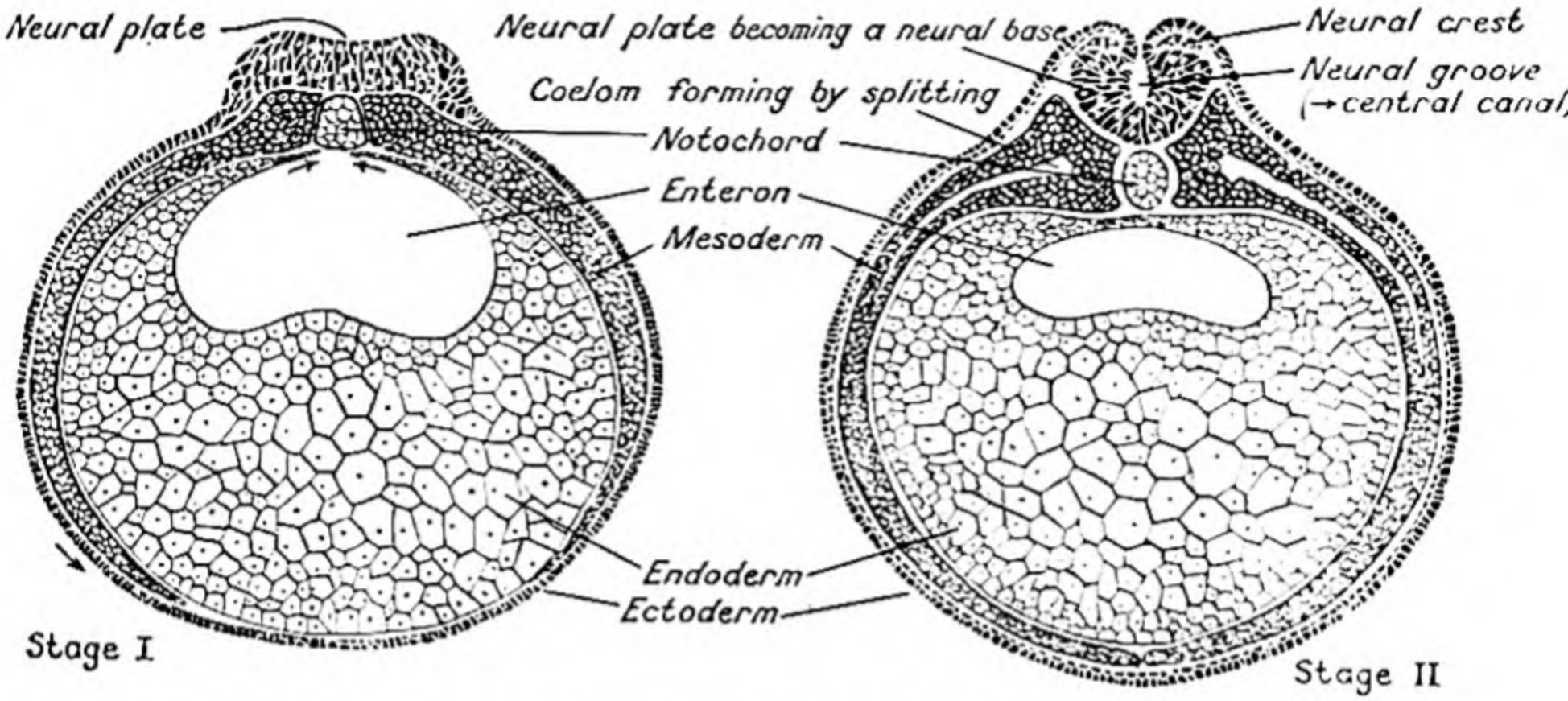


FIG. 299 – *Rana*. Transverse sections in the trunk region of stages in the development of the neurula.

cerned with the formation of the nerve-cord, for a portion on either side gets carried up to lie at the dorso-lateral edge of this structure, where it forms a **neural crest**, later giving rise to the afferent fibres of the nerves which are in connexion with the nerve-cord.

Presumptive Areas and Organisation

It has been demonstrated by micro-surgical methods that certain parts of an embryo, even during incipient gastrulation, are already irrevocably predetermined to behave in a particular way. Thus it is possible to remove fragments of tissue and graft them into an unaccustomed position, where they will often behave as if no such transplantation had occurred. Examples of such **presumptive areas** are afforded by the skin, neural plate and mesoderm. Thus if presumptive mesoderm be removed and grafted elsewhere in the embryo it is found to become invaginated, forming a blastopore in its new station, whilst presumptive neural plate will give rise to neural folds. In these cases, therefore, the tissue of each graft is undergoing **self-differentiation**. Its fate depends on its own composition and not on its position in the embryo.

But the micro-surgical operations of Spemann, performed on two species of newt, *Triton cristatus* and *Triton taeniatus*, have shown that powers of self-differentiation do not arise right at the outset of development. The species in question were chosen largely because the former lays a white egg, whereas the latter's egg is darker in colour. These

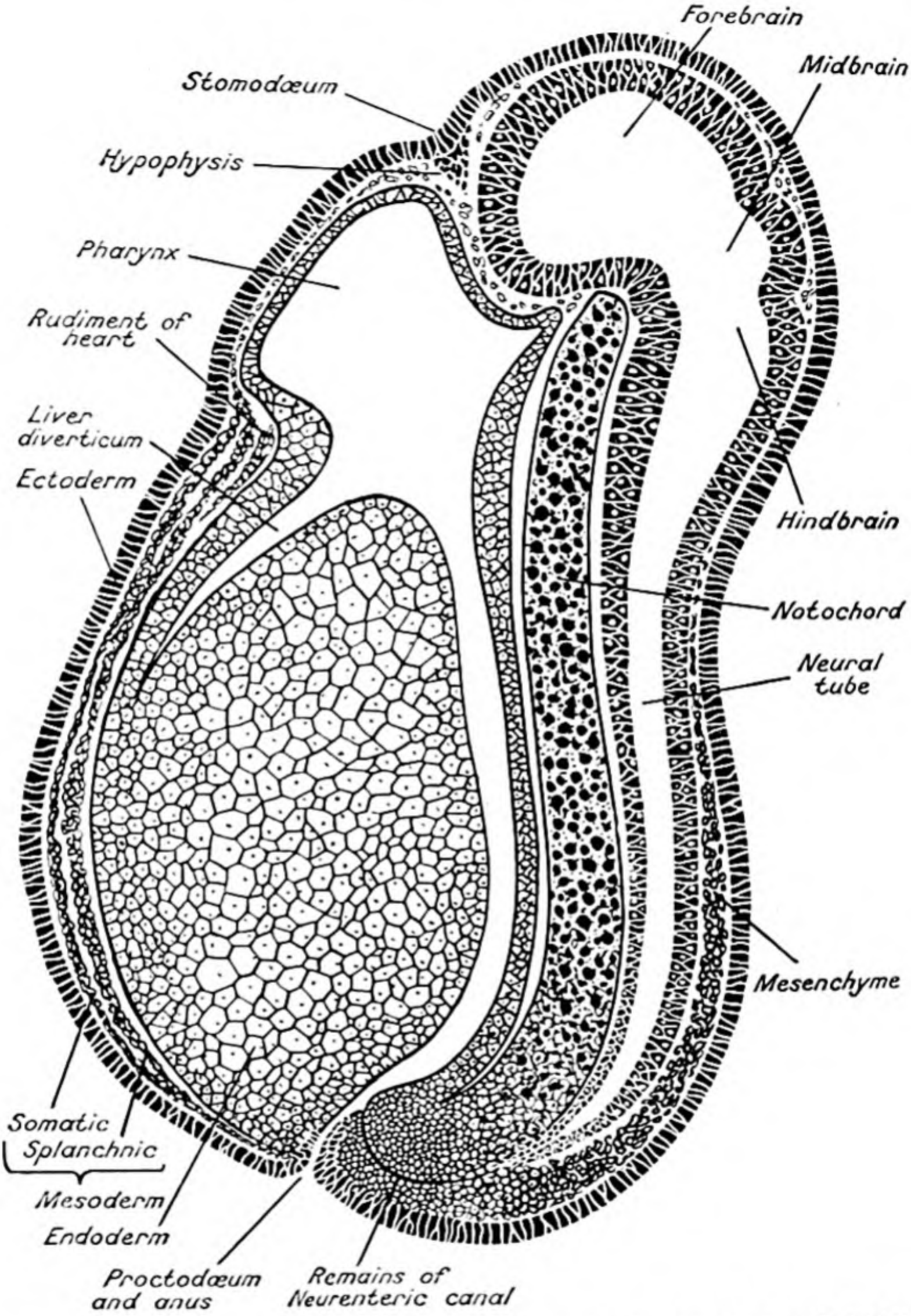


FIG. 300 – *Rana.* Longitudinal section of the late neurula stage (prior to hatching).

differences in coloration remain in the embryos, so that the fates of tissues transplanted from one into the other can be watched. Pieces of presumptive skin and neural plate were interchanged between members

of the two species. If this were done in the early gastrulation stage the fate of each was found to depend on its new position, and was not previously determined. A similar experiment performed upon late gastrulae showed the opposite result, the presumptive neural plate becoming neural plate and the presumptive skin giving rise to skin, despite their incongruity of position. Self-differentiation is apparently fixed in time to the period of gastrulation. It remained to discover the position in space of the determiner which was responsible for the development of the

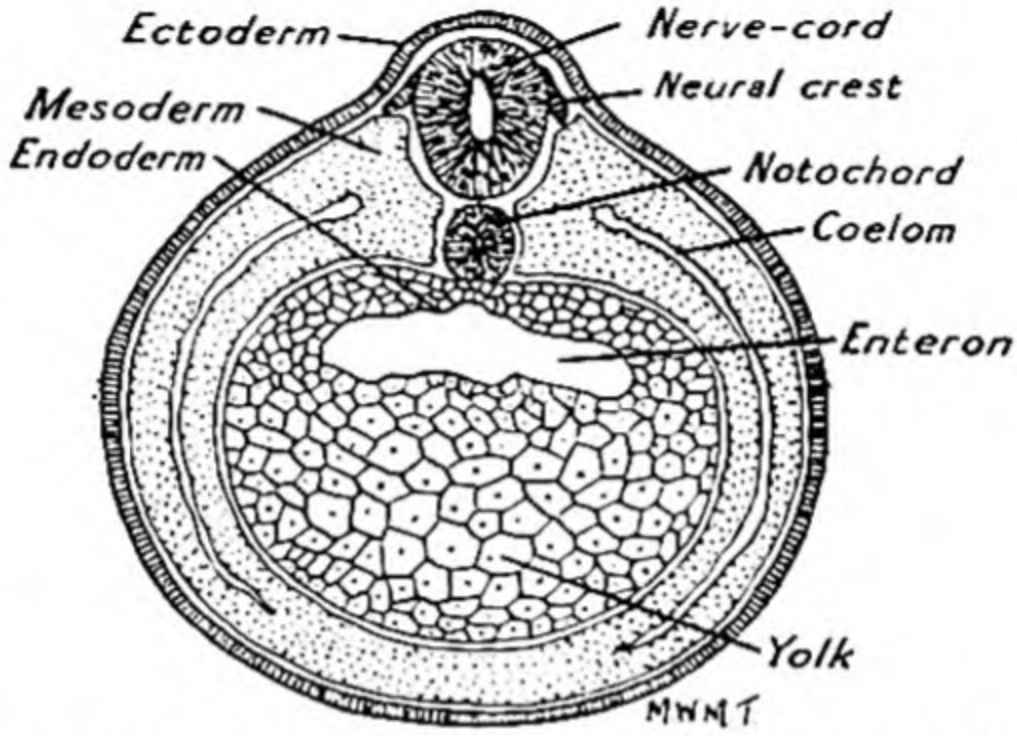


FIG. 301 – *Rana*. Transverse section, showing further formation of coelom.

powers of self-differentiation. This was proved experimentally to be located in the region of the blastopore. Spemann removed the blastopore region from a young gastrula of the species *cristatus* and grafted it into the ventral surface of a similar gastrula of a *taeniatus*. The latter, having now two blastopores, was found to develop two neural plates, as well as two lots of mesoderm. But the mesoderm formed as a result of the presence of the second (*cristatus*) blastopore was light in colour, signifying that it had actually been formed from this new blastopore, as was its presumptive fate, but the second neural plate was formed from host tissue. Thus its development had been induced from presumptive skin. Such structures whose fate depends on the presence and position of other tissues are said to undergo **dependent differentiation**. It has since been shown that the whole ring of mesoderm which lies in front of the blastopore acts as a determiner, though its influence weakens as it gets farther from the blastopore. Such a portion of the embryo acting as a determiner is called an **organisation centre**. Contact is essential for the spread of the influence of the organiser, as is evident from the fact that a suitable cut will prevent its exerting the customary effect. Although the experiments quoted above were performed on *Triton* the principles involved may be taken to apply equally well to the frog.

More recently, experimental evidence has been accumulated to suggest that the earliest determiner lies in the cortex of the egg. Thus, using the fertilised eggs of the amphibian *Xenopus laevis*, it was found that if extra grey crescent were grafted on to the opposite side of a fertilised egg, two sets of gastrulation movements occurred, giving rise to a double embryo. It was inferred that the additional grey crescent cortex induced the formation of a second blastopore dorsal lip, itself a known organiser. This was substantiated by the fact that the excision of the grey crescent area, while not interfering with cleavage and mitosis, completely prevented any orderly development. On the other hand, the removal of the grey crescent area at or after the 8-cell stage did not prejudice further development. It must be assumed that, by this time, its influence has spread irrevocably to parts under its control. It appears probable that the cortex is a self-replicating system, especially since cells of the grey crescent area (in investigated Amphibia) are known to be direct antecedents of the future germ-cells. It may well be that the grey crescent is somehow responsible for the mapping out of precisely biochemically differentiated areas of the fertilised egg, thus determining their fates and the subsequent distribution of the products of cleavage. For further information on this topic the reader is referred to the article by Dr A. S. G. Curtis in *Endeavour*, Vol. XXII, No. 87, September 1963 (I.C.I.).

Specific Adhesion

At this point reference may well be made to another phenomenon held to play an important part in the developmental process. Known as **specific adhesion**, it suggests that the many changes which result from the movements of cells, singly or collectively, from one part of the embryo to another, are due to alterations in the adhesive properties of cell-surfaces. When this adhesion fails the cells are free to move; when it operates they will be held in a fixed position. Thus during gastrulation in *Rana* there is a mass migration of superficial cells over the dorsal lip of the blastopore. But later these cells adhere again in groups – e.g., blocks of muscle, or notochord. By such movements, accompanied by growth, the basic plan of adult structure is achieved.

But the same phenomenon may be held to account also for the refinements of development. Thus, as parts of the embryonic ectoderm sink below the surface to give rise to the central nervous system, so certain associated cells migrate to various points where they form the receptor organs of the skin. Furthermore, extended projections from some nerve-cells migrate, often for appreciable distances, away from the bodies of the cells, and in this way nerve-fibres are formed.

Such specific adhesion as may account for developmental phenomena of the type instanced above must itself presumably depend upon the nature of the contacting surfaces of the cells. It may be that they are of highly specific protein nature, some pairs of which will adhere, whilst

others will not. In view of the almost infinite variety of protein structure, this would appear plausible. A parallel may be drawn from the specific nature of antigen-antibody reactions.

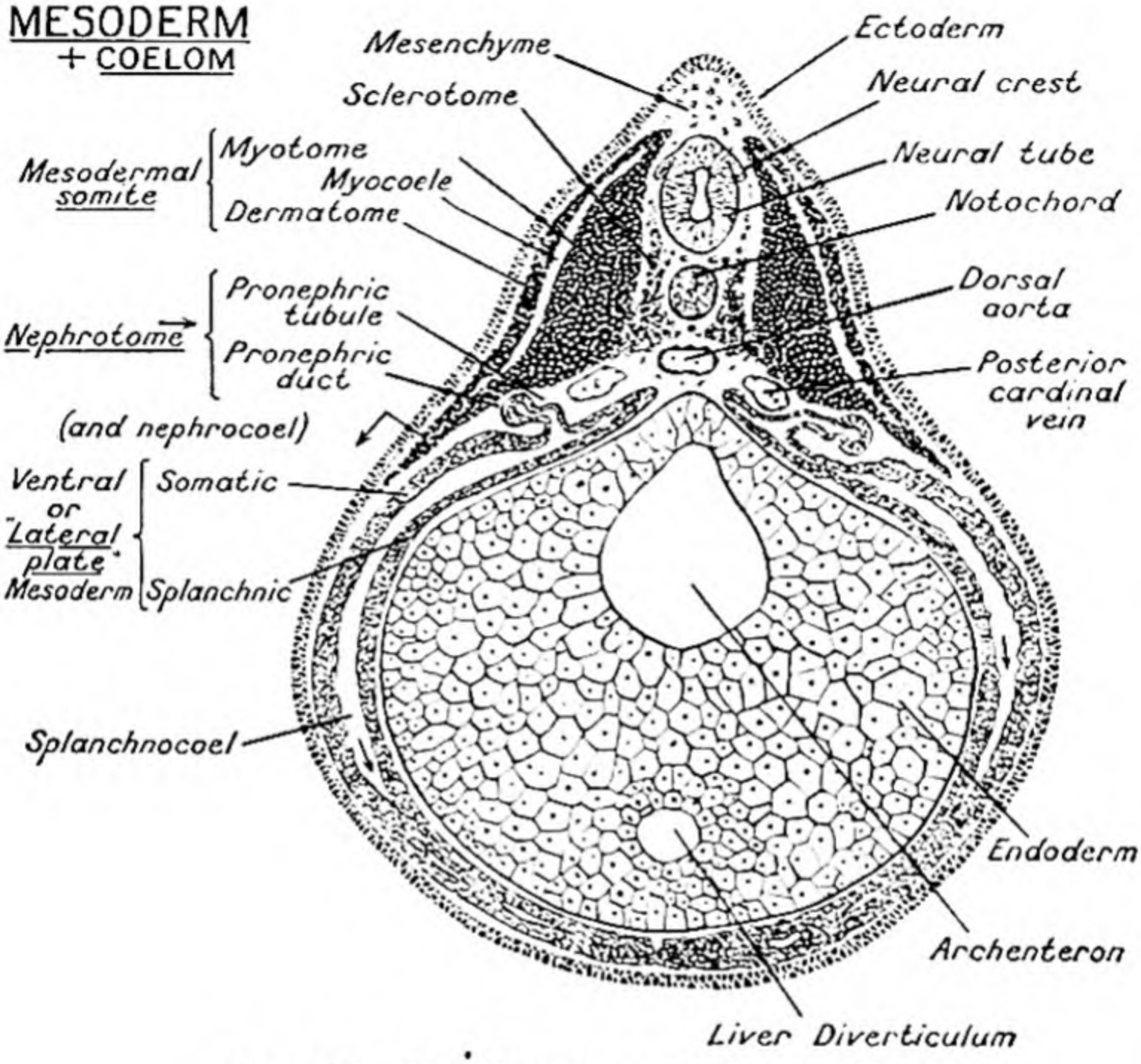


FIG. 302 – *Rana*. Transverse section, showing formation of nephrotome.

The problem of *direction* of migration is also evident. It has been suggested that it might well depend upon the polarity of the medium through which the migration occurs. If so, it remains to be discovered what induces the polarity.

For further information on this subject the student is recommended to read *Science News*, No. 13 (Penguin Books) and the appended bibliography.

Segmentation

As in *Branchiostoma* the embryo later becomes divided transversely into segments, this being most evident in the case of the mesoderm. Again as in *Branchiostoma* this process takes place only dorsally, and occurs from the front backwards. The inner wall of the mesoderm of this region

becomes thickened to form the muscular coat of the body-wall, and each portion, separated transversely from that in front of and behind it, is a **myomere**. The portion of the mesoderm which becomes thus segmented is known as the **vertebral plate**, or **somite**, whilst the ventral, unsegmented region is the **lateral plate**. Connecting the two, and corresponding in position to each myomere, is an intermediate cell-mass, or **nephrotome**, the cavity of which is termed a **nephrocoel**. Eventually the lateral plate becomes completely cut off from the vertebral plate, the musculature (myomeres) of which now extends ventrally to give rise to the muscles of the ventral part of the body-wall, and in some cases to those of the limbs. Corresponding to each myomere arises a ventral root (Chapter 26) of a nerve, whilst the neural crest also becomes segmented on a similar basis to give rise to the dorsal roots. Thus muscles and nerves display the same metameric segmentation, and it is indeed from the latter that segmentation may sometimes be traced where otherwise it has become almost completely obscured, as is the case with the vertebrate head.

Since, as has been stated, the nerves are segmental in arrangement, it follows that the vertebrae must be of segmental origin, for they alternate regularly with the nerve-roots. They arise, in fact, from cells, known collectively as **mesenchyme**, budded off from the inner sides of the myomeres. Some of these become arranged about the nerve-cord and notochord in the form of masses, termed **sclerotomes**. Also, separated from the outer side of each myomere is a **dermatome**, spreading out laterally to form the dermis of the skin.

Kidneys

The kidneys also are of segmental origin, arising from certain nephrotomes, mentioned above. On each side the nephrotomes of the second to fourth segments of the trunk become modified to form ciliated funnels communicating with the coelom. At their outer ends they are in connexion with a rod of cells, extending backwards between the ectoderm and the somatic mesoderm as far as the rectum. Eventually this rod of cells becomes converted into a tube, opening into the cloaca. Thus at this stage there is established a direct communication between the coelom and the exterior through the cloaca. These coelomic funnels (**coelomostomes**) and associated tubules constitute what is known as the **pronephros**, and the tube connecting them with the cloaca is the **pronephric duct**. The pronephros itself becomes somewhat enlarged as a result of the elongation of the tubules, whilst the tubules receive branches from the dorsal aorta and posterior cardinal veins, disposed by this time somewhat as in the dogfish. This structure remains as the functional kidney in the embryo and early larva, but later degenerates and disappears. It is replaced by the functional kidney of the adult, known as a **mesonephros**. This is formed from the nephrotomes of some six segments on either side, a little distance behind the pronephros. Coelomostomes are formed, and

the tubule of each grows outwards to open into the pronephric duct already present. From this point onwards it becomes known as the **Wolffian duct** and loses its connexion with the pronephros. The tubules of the mesonephros become very much branched and their blind endings

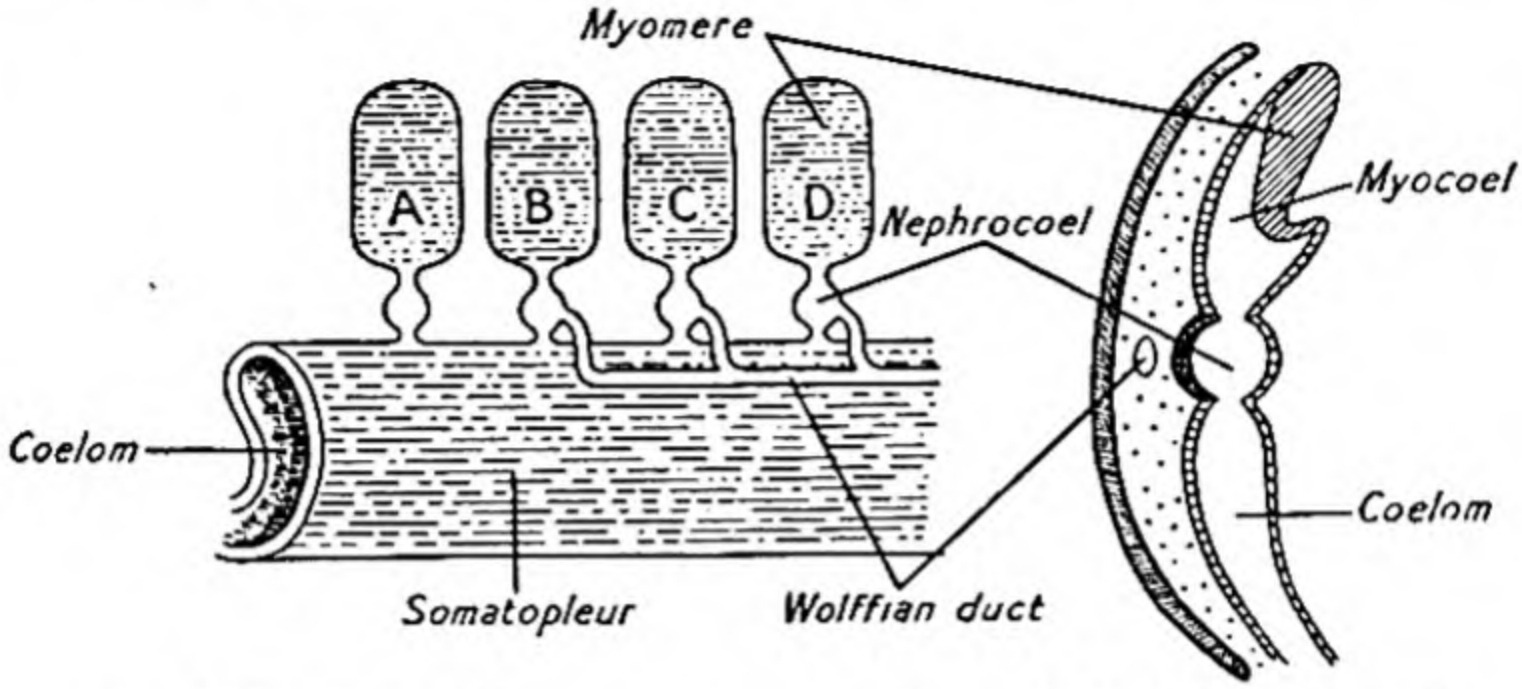


FIG. 303 – *Rana*. Diagram to represent the method of formation of the kidney tubules and Wolffian duct.

become invaginated to form cup-shaped vesicles, known as **Bowman's capsules**. Into each extends a minute branch of the dorsal aorta and of a posterior cardinal vein, and within the capsules these break up to form a network of capillaries, known as a **glomerulus**. Bowman's capsule and glomerulus together constitute a **Malpighian corpuscle**. Blood from the hind end of the body is carried to the kidneys on its return journey to the heart, so that the posterior region of each posterior cardinal vein becomes the renal portal vein.

Gonads and their ducts

In close association with the kidneys are the ducts of the gonads. The gonads themselves arise as evaginations of coelomic epithelium at the dorso-median corners of the splanchnocoel. In these evaginations arise strands, containing the primordial germ-cells. In embryos destined to become males these strands become hollowed out and establish connexion with the tubules of the mesonephros. Thus the vasa efferentia are formed, and the spermatozoa produced later pass along these tubes to reach the exterior via a Wolffian duct.

But the eggs are not passed along a ready-made duct, so that in the female a pair of **Müllerian ducts** arises to act as oviducts. Each Müllerian duct arises in the form of a longitudinal groove in the wall of the coelom to the outer side of the gonad. It lies parallel to and extends the length of the pronephric duct. This groove becomes folded over to form a tube which communicates anteriorly with the coelom by the pronephric funnels of the early larva, whilst posteriorly it opens into the cloaca. The

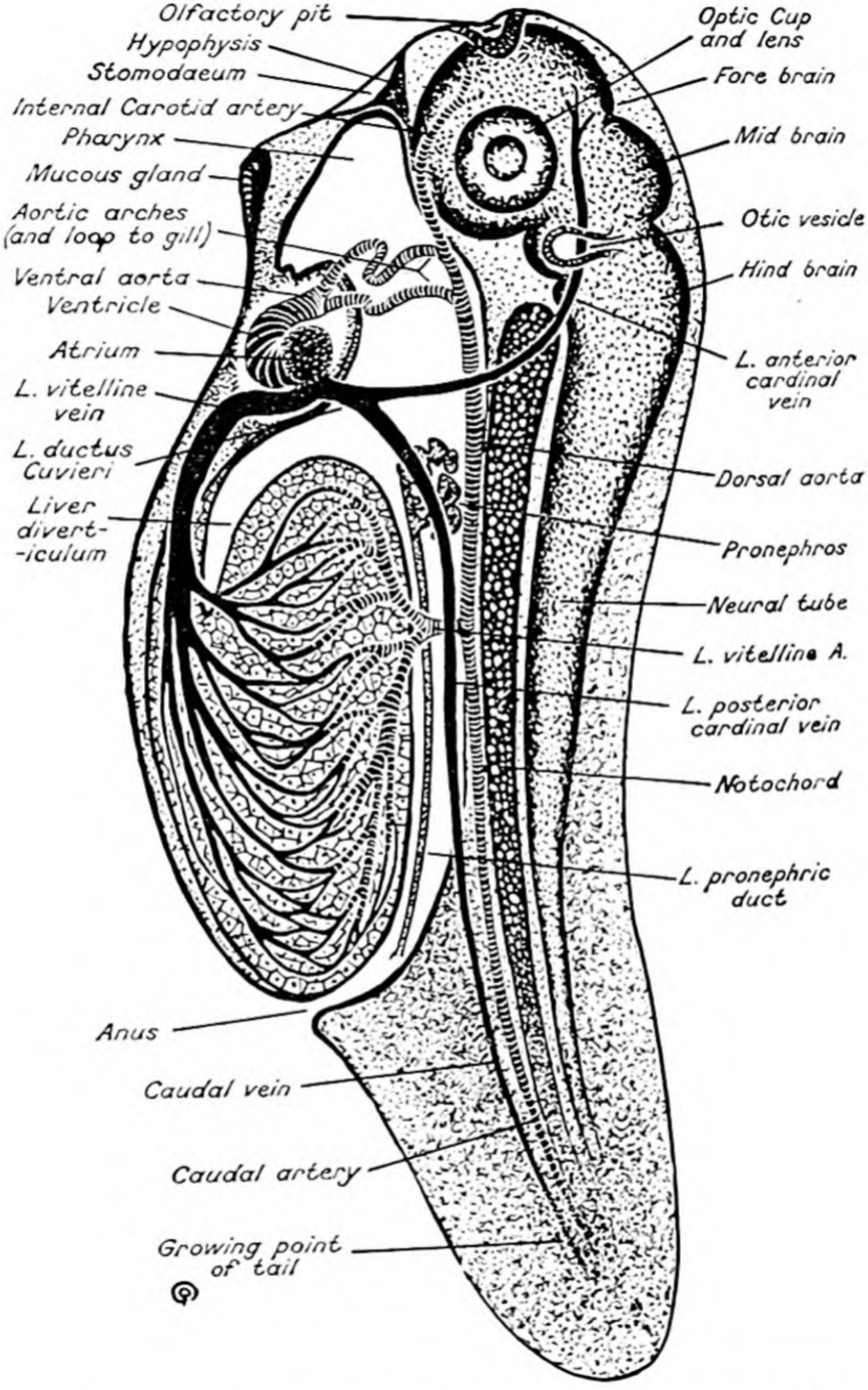


FIG. 304 – *Rana.* Tadpole at time of hatching, shown as a transparency.

Müllerian ducts are represented in the male, but later degenerate and disappear.

Alimentary Canal

This is formed from the original archenteron and is completely closed in by endoderm. In the posterior part there is, for a long time, a collection of yolk-cells. Gradually the whole becomes regionally differentiated to form the divisions characteristic of the adult, but in the earlier stages it is the perforation of the gill-slits in the pharyngeal region which is of most importance. Five pairs of visceral clefts are formed by evagination of endoderm and slight invagination of the ectoderm opposite. The first pair of pouches represents the spiracles of *Scyliorhinus*, but in the frog they never become perforated, though their cavities remain as the Eustachian tubes. The remaining four pairs eventually become perforated to form gill-slits. But respiration is first effected not by these true internal gills but by external gills, of which there are three pairs, arising as dorsal outgrowths from the third, fourth and fifth visceral arches (i.e., the arches behind the first, second and third true gill-slits). They become richly vascularised. In this same region arise two important ductless glands. The **thyroid** is formed as a depression in the floor of the pharynx, between the second gill-slits. It loses its connexion with the cavity of the mouth and pours its secretion into the blood. It eventually becomes bi-lobed. From the roof of the first gill-slits arises the **thymus** gland as a downgrowth, in the same way as does a tongue-bar from the primary gill-slits of *Branchiostoma*. Thus the thymus gland is said to be homologous with the tongue-bars of *Branchiostoma*. Posterior to the thyroid gland a ventral diverticulum of the pharynx gives rise to the **larynx**. This forks and each free end becomes expanded to form a lung. The liver arises behind the larynx as a ventral diverticulum, which becomes enlarged and lobulated. It retains its connexion with the alimentary canal by the bile-duct, near the opening of which arises the pancreas as an outgrowth from the gut. Finally a ventral diverticulum from the rectum becomes bi-lobed to form the urinary bladder.

The whole gut is suspended in the coelom, being covered by the splanchnic mesoderm except in the mid-dorsal line and separated from the somatic mesoderm by the coelomic cavity, containing coelomic fluid. The wall of the coelom in the abdominal region becomes known as the **peritoneum**. In the mid-dorsal line the inner walls of the coelom become closely applied to form the **dorsal mesentery**. This mesentery becomes specially folded to support the various diverticula of the gut, as well as the heart and principal blood-vessels. The coelomic cavity containing the heart becomes separated off from the remainder of the coelom in which the gut is suspended (perivisceral or peritoneal cavity). The chamber enclosing the heart is the **pericardial cavity.**

Vascular System

A number of mesoderm cells between the floor of the gut and the splanchnic mesoderm by which it is suspended become arranged in the form of a tube, known as the **subintestinal vessel**. Behind the pharynx this is at first double, but the component halves soon merge and the cells in this region lay down the lining tissue of the heart – the *endocardium*. The muscular wall of the heart – the *myocardium* – is laid down by more cells from the splanchnic mesoderm, enveloping the endocardial tubes. As the tube lengthens it is thrown into an S-shaped bend, whilst later the more posterior loop is pushed forwards to lie dorsal to the anterior portion. The chambers are made by dilations of the wall. At the posterior end is the sinus venosus, receiving blood from the two vitelline veins (see below). In front of this are the atrium, ventricle and conus arteriosus. Before hatching the chambers are not fully formed, whilst the valves and partition dividing the atrium into two auricles are not established. Even in this condition pulsations of the heart muscles may be observed. The **dorsal aorta** is of paired origin, the lateral aortae which comprise it remaining separate in front and uniting posteriorly. At this stage the vascular system is essentially that of a fish. A **ventral aorta** extends forwards from the heart, and from this structure four pairs of **afferent branchial** vessels extend into the third to the sixth visceral arches, supplying them with blood for oxygenation at the gills. Four pairs of **efferent** vessels carry this blood to the lateral dorsal aortae for distribution. In the first two visceral arches transitory aortic arches appear.

Veins are formed in a similar manner. A pair of **vitelline** veins returns blood to the heart from the liver and yolk-cells, whilst on either side of the dorsal aorta lies a **posterior cardinal** vein. Each extends forward to form the **anterior cardinal** vein. Now both anterior and posterior cardinal veins lie in the body-wall, and are thus separated from the heart by the coelom. But in the region of the heart a shelf grows inwards from the somatapleur on either side and outwards from the splanchnopleur opposite. These meet and fuse to form the transverse septum, cutting off the pericardia from the remainder of the peritoneal cavity. It is across this transverse septum that a **ductus Cuvieri** is developed on either side to establish communication between the heart and the cardinal veins. These ductus Cuvieri eventually become the **anterior venae cavae**, whilst a **posterior vena cava** is developed in the dorsal mesentery. Finally, each of the vitelline veins becomes subdivided into an anterior and posterior region. The former connects the liver with the heart and is known as the **hepatic** vein, whilst the posterior region conveys blood from the gut to the liver, and thus forms the **hepatic portal** vein. Each posterior cardinal vein later becomes interrupted on its journey back to the heart, for it penetrates the kidney of its own side and thus the portion of it posterior to this organ is the **renal portal** vein.

During the process of metamorphosis, later to be described in more detail, important changes occur with regard to the arteries in particular, for these must be so modified as to accommodate respiration by lungs instead of by gills, though lungs are used as the principal respiratory

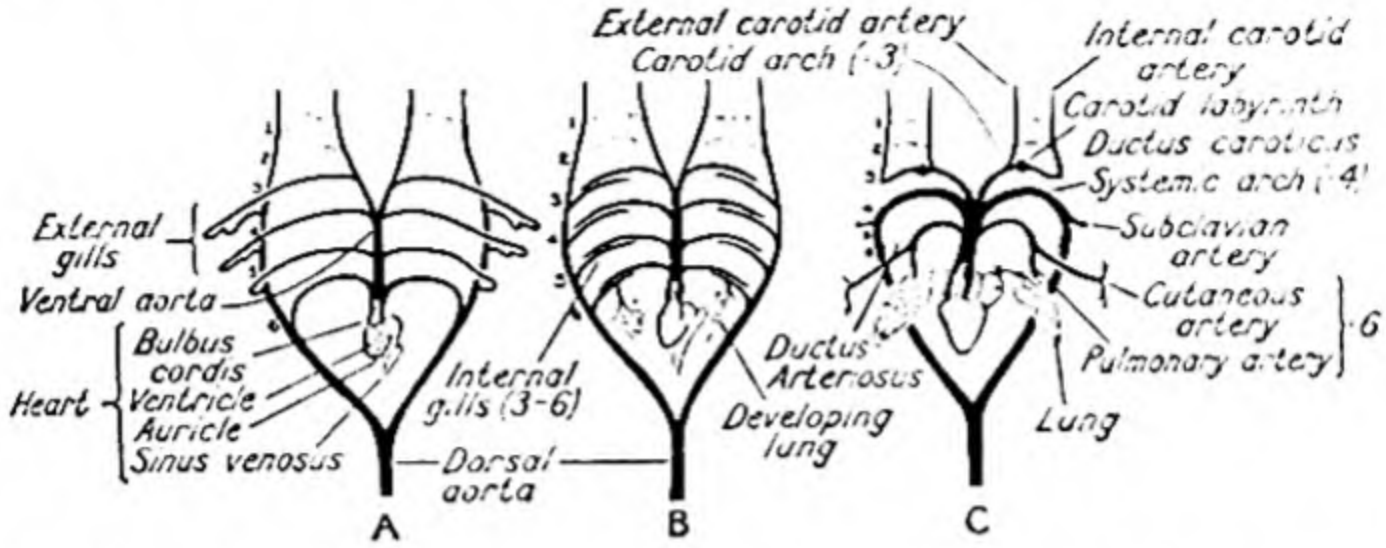


FIG. 305 – *Rana*. Changes in the arterial arches during development (diagrammatic). *A*., External gill stage; *B*., Internal gill stage; *C*., Adult condition.

organs some time before metamorphosis. The blood-supply to the gills becomes very much reduced by the establishment of direct connexions between afferent and efferent branchial arches, whilst from the vessel of the sixth arch on either side a branch passes to the rudimentary lungs, so that in this way a **pulmonary** artery is formed. The vessels of the fourth become the **systemics** and those of the third the **carotids**. The vessels of the first two arches are only transitory and now disappear completely, as also do those of the fifth branchial arch. Finally all dorsal connexion between the pulmonary, systemic and carotid arches, previously effected by the lateral dorsal aortae, is lost, so that the arterial system is now practically of adult form. The relationships between the arterial systems of the tadpole at the external gill stage and the internal gill stage and of the adult will be made clear by a careful study of Fig. 305.

External Features

In conclusion the changes which are visible externally during the development of the frog will be considered. These are sharply divisible into those of the earlier development up to the fully-formed tadpole stage and those which accompany metamorphosis.

(A) DEVELOPMENT OF THE TADPOLE. At first the embryo is spherical, but soon becomes elongated, a distinct head region becoming visible as a result of a slight constriction. This is the point at which the neurula stage is reached (page 511). At the same time the future position of the eyes, nostrils and gills may be discerned, the last-named being represented as a distinct bulge, representing the *gill plate*. Somites are visible and occasional twitchings may be observed as they contract. The ectoderm is ciliated and the embryo slowly rotates within its membrane.

After about two weeks this embryo escapes from the jelly in which it is embedded, and soon there may be distinguished rudimentary eyes and nostrils, and a groove denoting the future position of the mouth. Behind this groove is a rounded, ventral **cement-gland**, by means of which the newly-hatched tadpoles attach themselves in clusters to objects in the water. If attached thus to water-weeds the tadpoles augment their supply

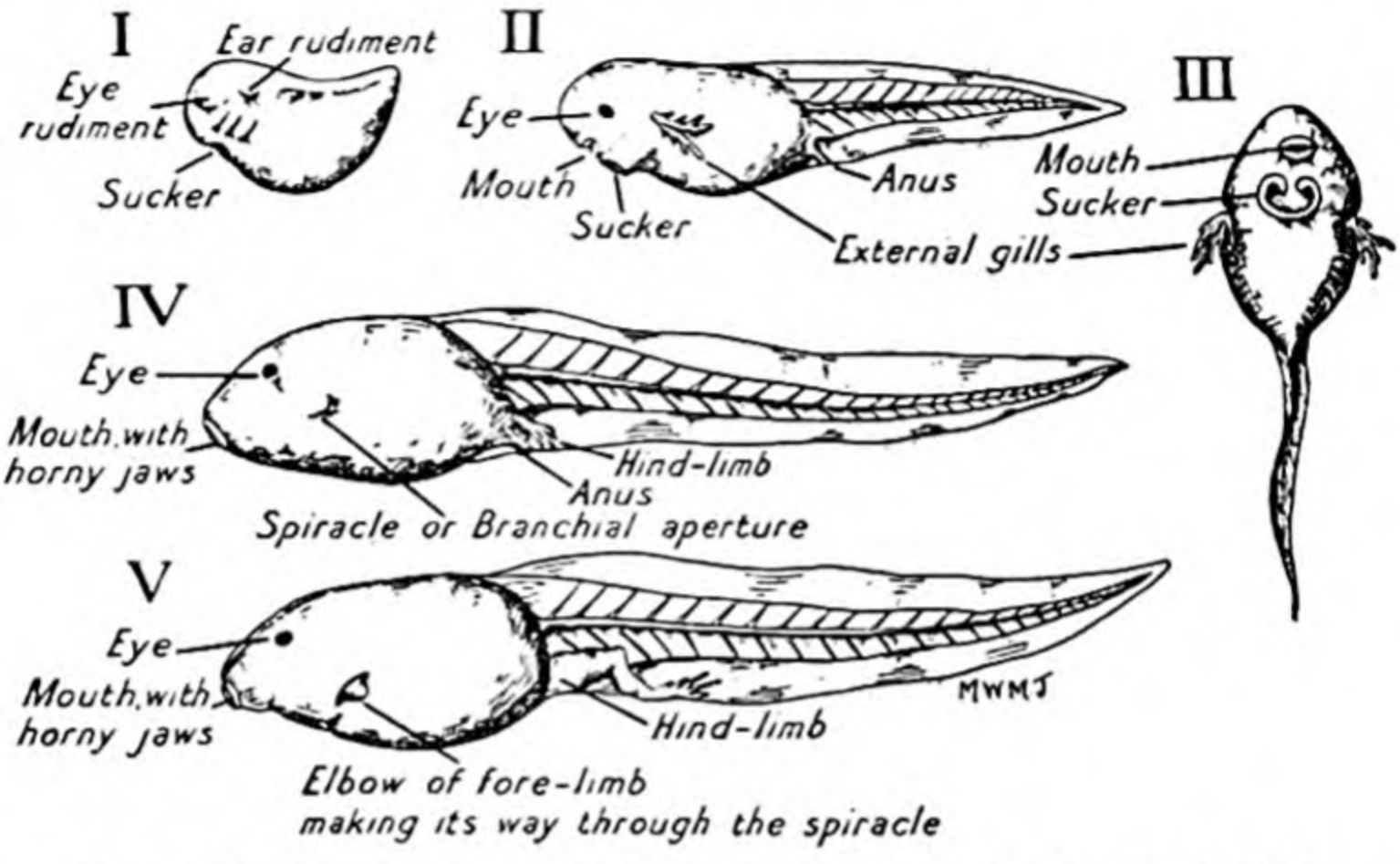


FIG. 306 – *Rana*. External changes during the development of the tadpole.

of oxygen, for by the process of photosynthesis the green plants are continuously liberating this gas in sunlight. On each side of the head two blunt projections appear, followed by a third. These become much branched and form the **external gills**. If a tadpole be examined under the microscope at this stage blood may be seen circulating in the filaments of the external gills. Together with the skin these gills effect respiration, for the surface of the body is ciliated and thus the water surrounding it is continuously renewed. Up to this stage food takes the form of the yolk of the original egg, lying now in the floor of the posterior end of the gut. About a week after hatching a mouth appears, bordered by a pair of horny jaws. The tadpole now feeds on minute plant organisms, and the gut may be seen by transparency through the body-wall as a coiled tube. At this time the **gill-slits** become perforated, four pairs in all, and on their walls these develop lamellae which become highly vascularised. A fold of skin now appears on either side, just in front of the most anterior gill-slit. These folds grow backwards and become fused behind the last gill-slits with the body-wall, except for a small **opercular spout** to the left of the mid-ventral line. Thus the gill-slits become completely enclosed within the **operculum**. The external gills gradually disappear as the

operculum grows over them, and the hind-legs are first discernible as small swellings, which later become regionally differentiated into the various parts of the limbs. The fore-limbs are also formed now, but at first they are obscured by the opercula. By about the twelfth week the left one has come to protrude through the opercular spout, whilst the right bursts through the operculum itself. At this time the tadpole may become in part carnivorous, whilst respiration, at first purely fish-like, may later become more adapted for life on land, for the tadpole may be seen frequently to rise to the surface and gulp in air, which enters the rudimentary lungs. This fully-formed tadpole is known as a **larva**, for it is a stage in the life-history of the frog, dissimilar in structure from the adult, but leading an independent existence. An **embryo**, on the other hand, is merely a stage in development incapable of feeding independently.

(B) METAMORPHOSIS. Larva-formation is almost always followed by something akin to **metamorphosis** – the series of rapid changes resulting in the assumption of adult form by the organism. Several clearly-defined changes occur in the tadpole. Thus the skin is cast after feeding has ceased. The horny jaws are shed and the gape of the mouth widens. In accordance with a change from herbivorous to carnivorous habits the gut shortens, for the food taken more closely resembles in chemical nature the tissues of the animal's own body and thus needs be changed less severely in the process of digestion. The gills eventually atrophy completely, whilst the tail is absorbed by the phagocytes of the blood. It is largely through this that the animal is nourished during this period of restraint from feeding. It is not until the third year of its life that the frog becomes sexually mature.

PRACTICAL WORK

Examine and draw any available microscopic preparations of stages in the embryology of the frog.

Examine the external features of as many stages as possible in the formation of the tadpole. Note first the relative pigmentation of the animal and vegetable poles, followed by investigation of structure as detailed on page 521.

Examine in water on a watch-glass under the low power the external gills of a living tadpole. It will be possible to distinguish the flow of blood through the capillaries.

Most conveniently, of course, the study of the external features of the development of *Rana* may be effected from specimens kept in an aquarium, though failing this they may be collected at intervals from neighbouring ponds.

CHAPTER 30

Embryology of Gallus and Oryctolagus

GALLUS

Fertilisation

The 'yolk' of a hen's egg is really one cell, largely composed of reserve food material and, at one side, a small area of clear cytoplasm, known as the **germinal disc** and containing a single nucleus. The yolk being thus concentrated at one pole, the egg, like that of the frog, is described as *telolecithal*. The yolk of the egg is immediately surrounded by a slender **vitelline membrane**, and is itself arranged in layers. The egg is liberated from the ovary (only the left ovary persists in birds) at the primary oöcyte stage and passes into an oviduct, along which it moves in such a way that its axis of symmetry is at right angles to the length of this tube. At copulation sperms are inserted by the cock into the base of the genital tract of the female, from which region they reach the upper end of the oviduct, where fertilisation occurs. During the passage of the fertilised egg to the exterior, albumen, inner and outer **shell-membranes** and the **shell** itself are secreted by the walls of the oviduct and plastered on to the egg. Between the two shell-membranes there occurs at the blunt end of the egg a small air-space. Owing to an axial rotation by the egg at this time the thickened threads, or **chalazae**, by which the rest of the egg is suspended in the albumen, become spirally coiled. Since the yolk is denser than the germinal disc the egg rotates within the albumen to bring the germinal disc to the top. Hence it is always nearest to the source of heat from the body of the incubating hen. The shell itself consists of horny matter, impregnated with the phosphates and carbonates of magnesium and calcium. Superficially there is laid down a variable amount of pigment. Thus the egg is self-contained, and from the outside demands only oxygen and a certain limited range of temperature for development to occur. Unlike the conditions in which the eggs of the frog and *Branchiostoma* develop, there is a limited supply

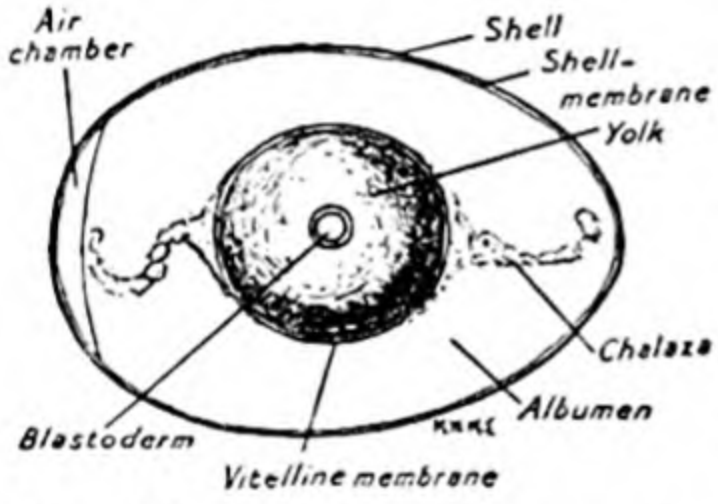


FIG. 307 – *Gallus*. The egg, seen by transparency.

even of water available, so that water-metabolism must needs be carefully regulated. For water-supply the frog's egg depends on its environment, which must contribute oxygen and a suitable temperature in addition. Since the shell and membranes are permeable to gases there is an adequate supply of oxygen available to the chick embryo. The albumen exercises certain anti-biotic effects and acts as a water reservoir.

Cleavage

So great is the quantity of yolk in the egg of *Gallus* that cleavage is only partial, or **meroblastic** – i.e. it is confined to the germinal disc. The first cleavage furrow appears at about the time when the albumen is being added to the egg, whilst by the time the shell has been formed it is at the 8-cell stage. When the egg is laid the blastula stage has been passed and a

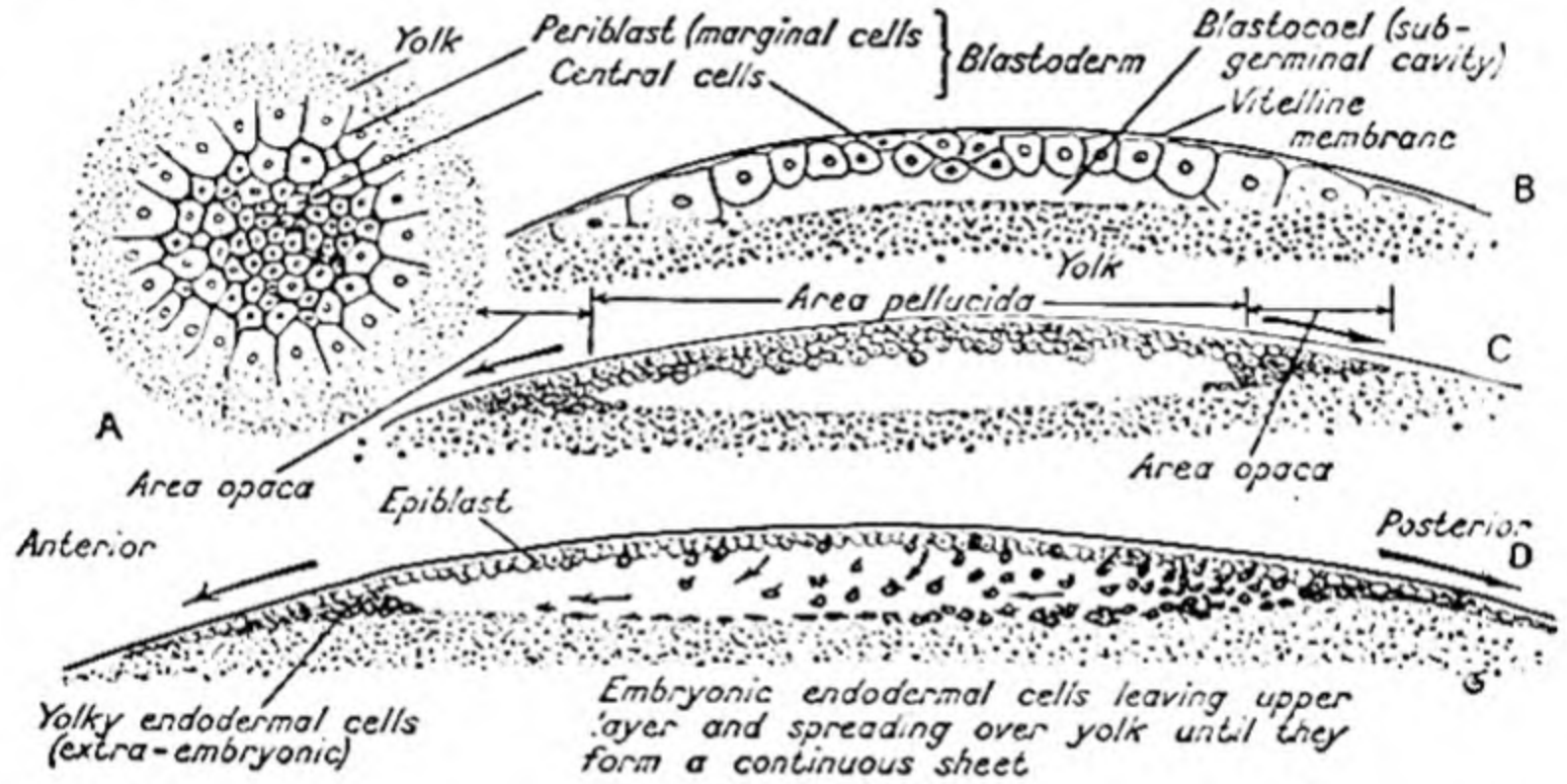


FIG. 308 – *Gallus*.
A., Surface view of early blastoderm; *B*., Vertical section of early blastoderm; *C*., Later stage; *D*., Later stage still, showing the spreading and thinning of the blastoderm and the origin and spread of the hypoblast.

certain amount of gastrulation has already occurred. Thus a certain amount of difficulty in obtaining the early stages of development is experienced.

The amount of cytoplasm is very small, and cleavage results in the formation first of a flat disc of cells, known as the **blastoderm**. Around its entire margin this merges into the yolk, from which it is separated beneath by a small cavity – the **blastocoel**. The circular zone where the blastoderm is continuous with the yolk is known as the **periblast**, which owing to its comparative opacity, is termed also the **area opaca**, in contrast to the clearer blastoderm within, called the **area pellucida**. The blastoderm later extends further over the yolk, so that the area opaca is increased in dimensions. The undivided yolk of the hen's egg may be regarded as the equivalent of the megameres of the frog.

Gastrulation

Hypoblast is formed by proliferation from a small sector of the posterior part of the embryonic area. As it extends laterally the superficial layer of cells, originally the blastoderm, now constitutes the **epiblast.** The hypoblast soon merges into the periblast. It is about at this stage that the egg is laid, some twenty-four hours having elasped since fertilisation.

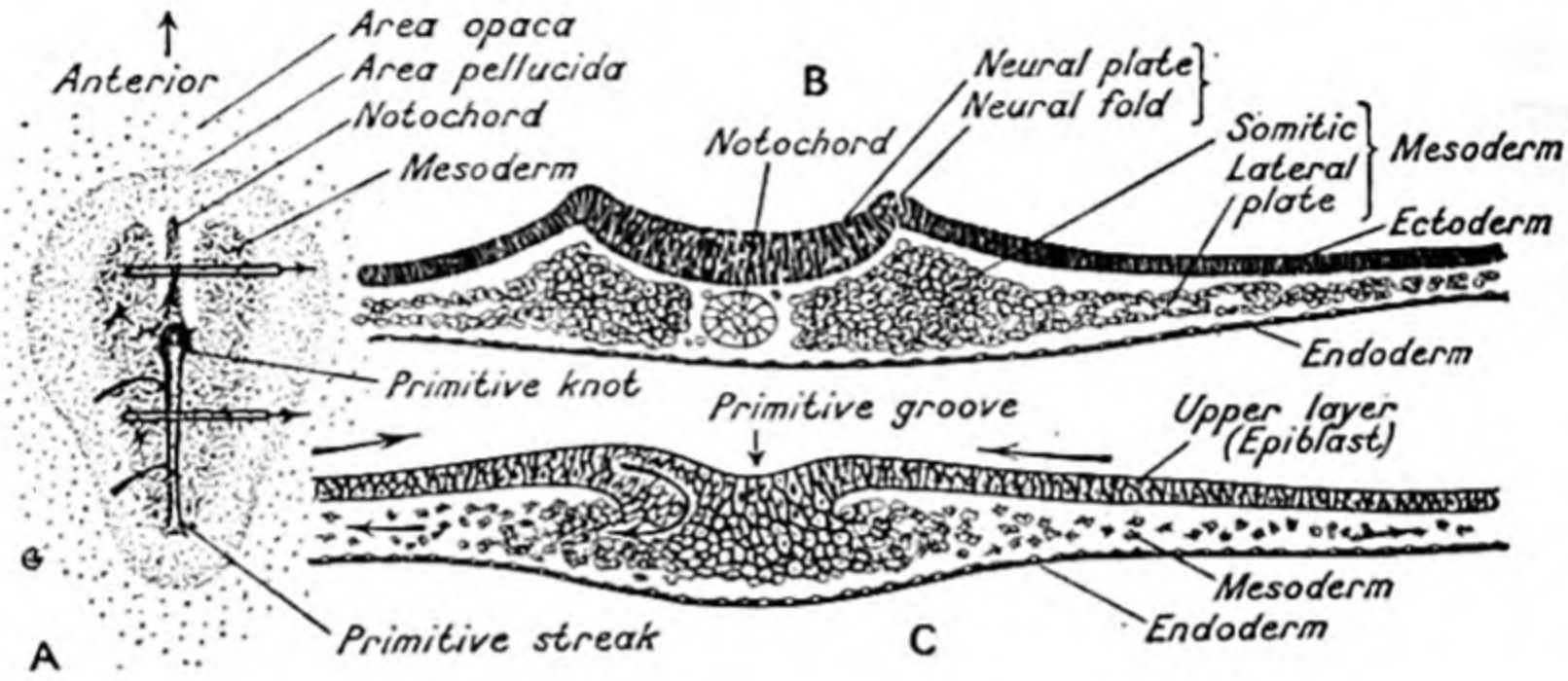


FIG. 309 – *Gallus.*
A., Blastoderm (area pellucida), showing early formation of mesoderm and notochord; *B.*, Transverse section anterior to primitive streak, showing formation of embryo. *C.*, Transverse section of primitive streak, showing movement and migration of cells;

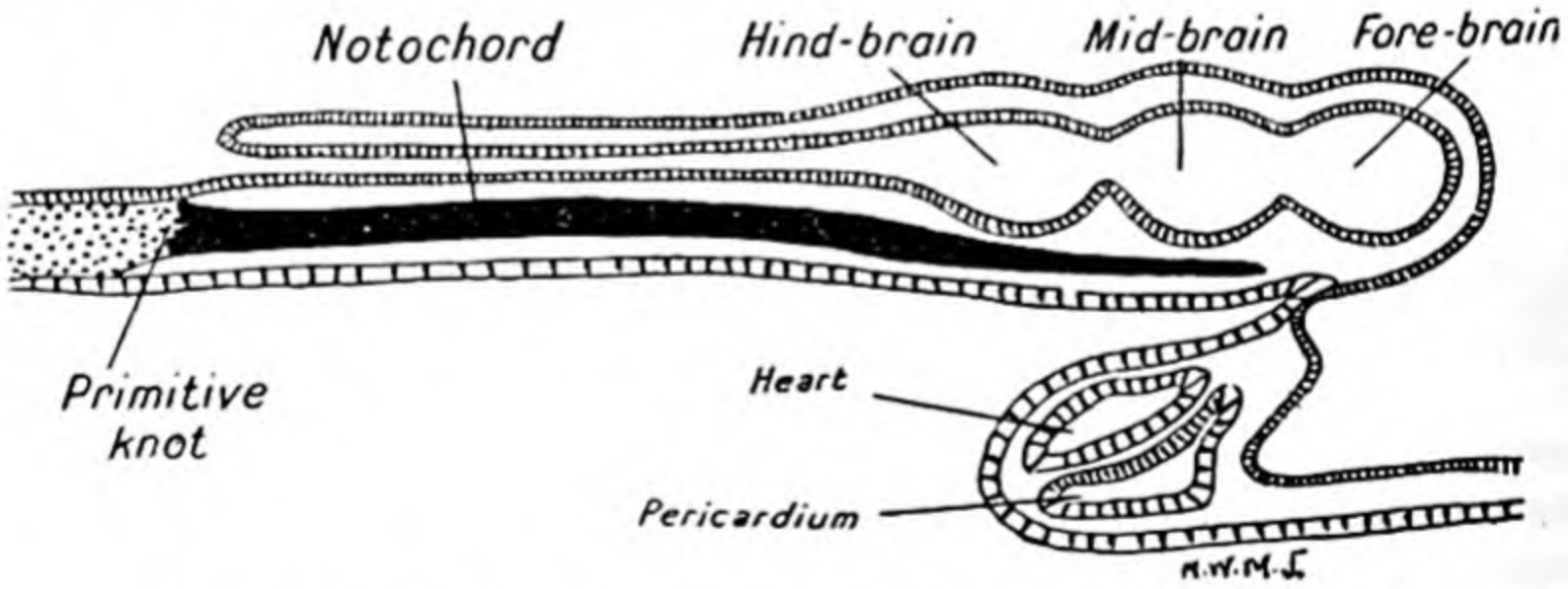
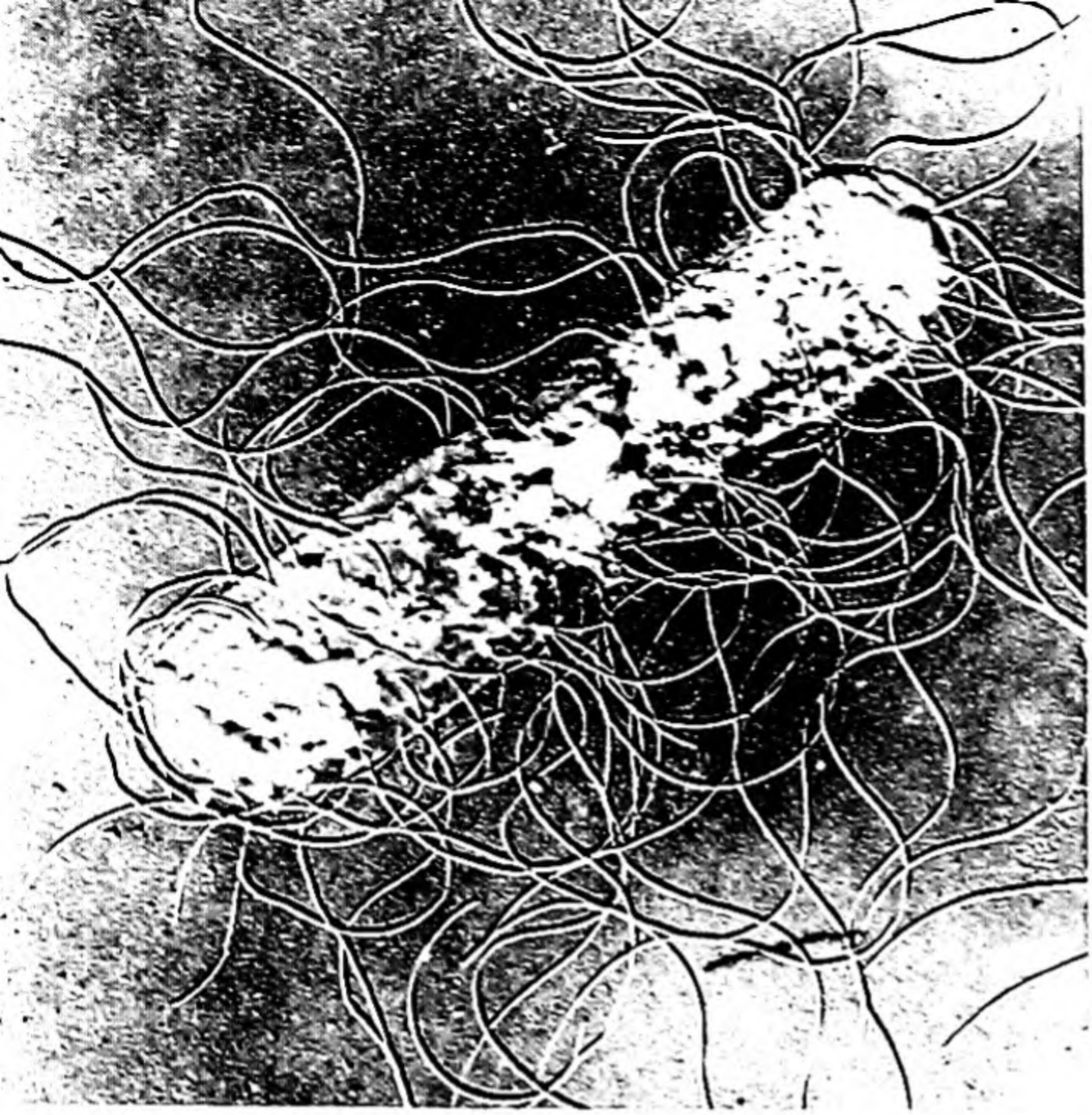


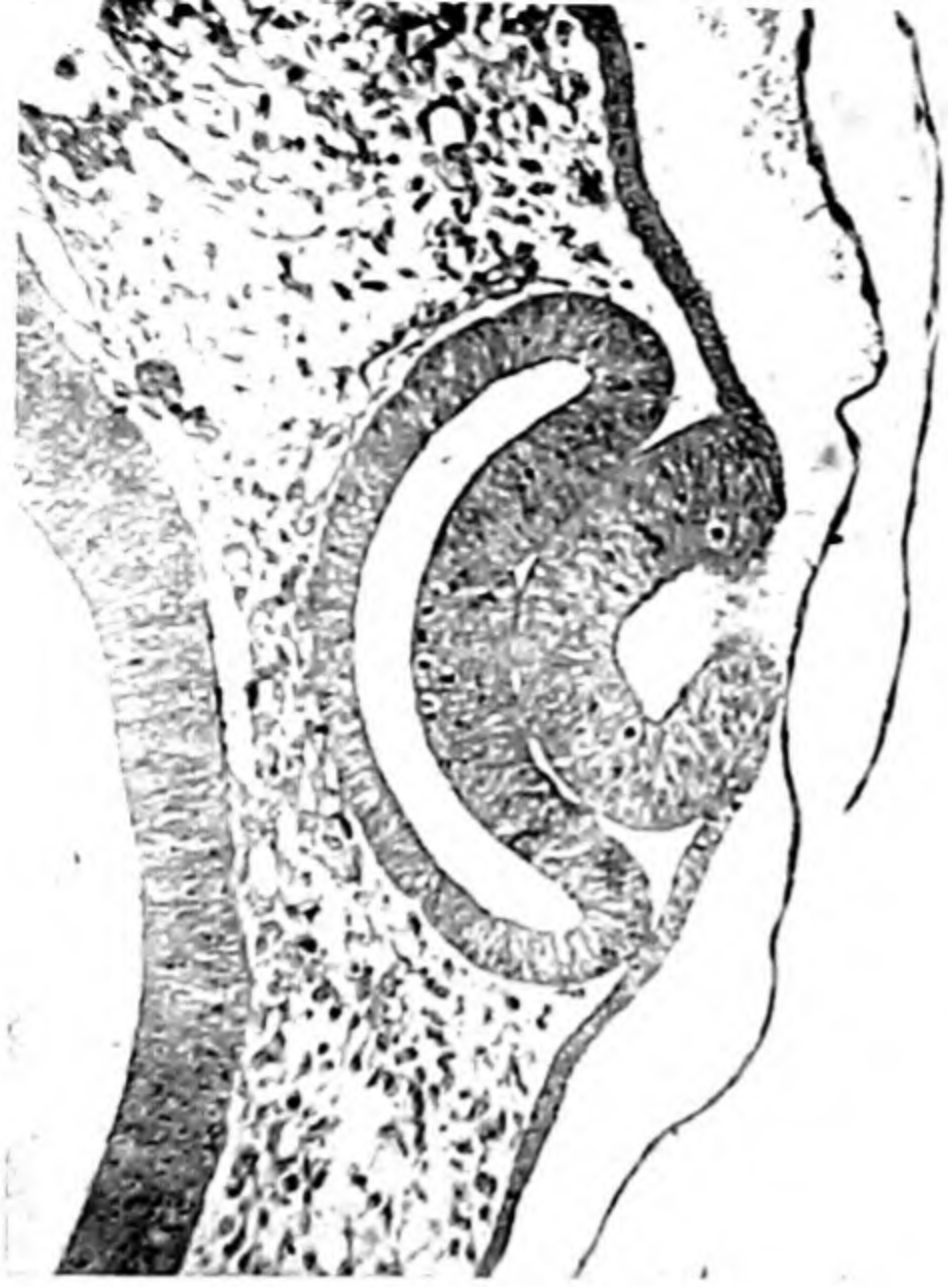
FIG. 310 – *Gallus.* Longitudinal section, showing formation of notochord. (After de Beer.)

By the migration of cells into the middle of the area pelludica there is now developed a thickening in the upper layer of the blastoderm, known as the **primitive streak**. This lies at right angles to the length of the egg and is formed from in front backwards. Along this primitive streak appears a shallow groove, ending anteriorly in the form of a blind pit. This is bordered on its anterior margin by a raised **primitive knot**. This primitive knot represents the dorsal lip of the blastopore of lower forms, whilst the walls of the groove represent the lateral lips of this same struc-



Proteus vulgaris (X 15,000). 'A species isolated from putrefying meat infusions, and abscesses. In certain infections of the digestive tract *proteus* has been frequently held to be the responsible agent. The real relation of *proteus* to intestinal infection is, however, still obscure.' (Quoted from 'The Pocket Medical Dictionary'.) (By courtesy of Messrs Upjohn Ltd.)

Blowfly eggs on teeth of rabbit. (By courtesy of the executors of the late Alan Dale and of Messrs Flatters & Garnett Ltd.)



Longitudinal section of head of mammalian embryo in the region of the fore-brain, showing rudiments of optic cup and lens.

Transverse section of mammalian oesophagus showing branched saccular glands.

Transverse section of testis of *Hydra*.

Hydra, showing testes and attached embry (gastrula stage).

ture. All that remains of the aperture of the blastopore is the pit and the groove of the primitive streak. By vital dye staining experiments it has been discovered that both the notochord and the mesoderm arise as a result of a superficial migration of cells. Cells destined to give rise to the former pass over the primitive knot and move forwards to form the **notochordal** (or *head*) **process**, whilst cells of the future mesoderm extend laterally between epiblast and hypoblast. At this time the primitive streak lengthens and the groove becomes deeper, whilst the whole area pellucida, previously circular, becomes pear-shaped. The primitive streak subsequently decreases in length, not so much as a result of the differentiation of mesoderm as by the exhausting of the supply of migrating cells; it is ultimately obliterated. Thus the gastrula stage is arrived at without the process of invagination.

Nerve-cord and Pro-amnion

During the formation of the notochordal process the epiblast overlying this structure and anterior to the primitive knot becomes a

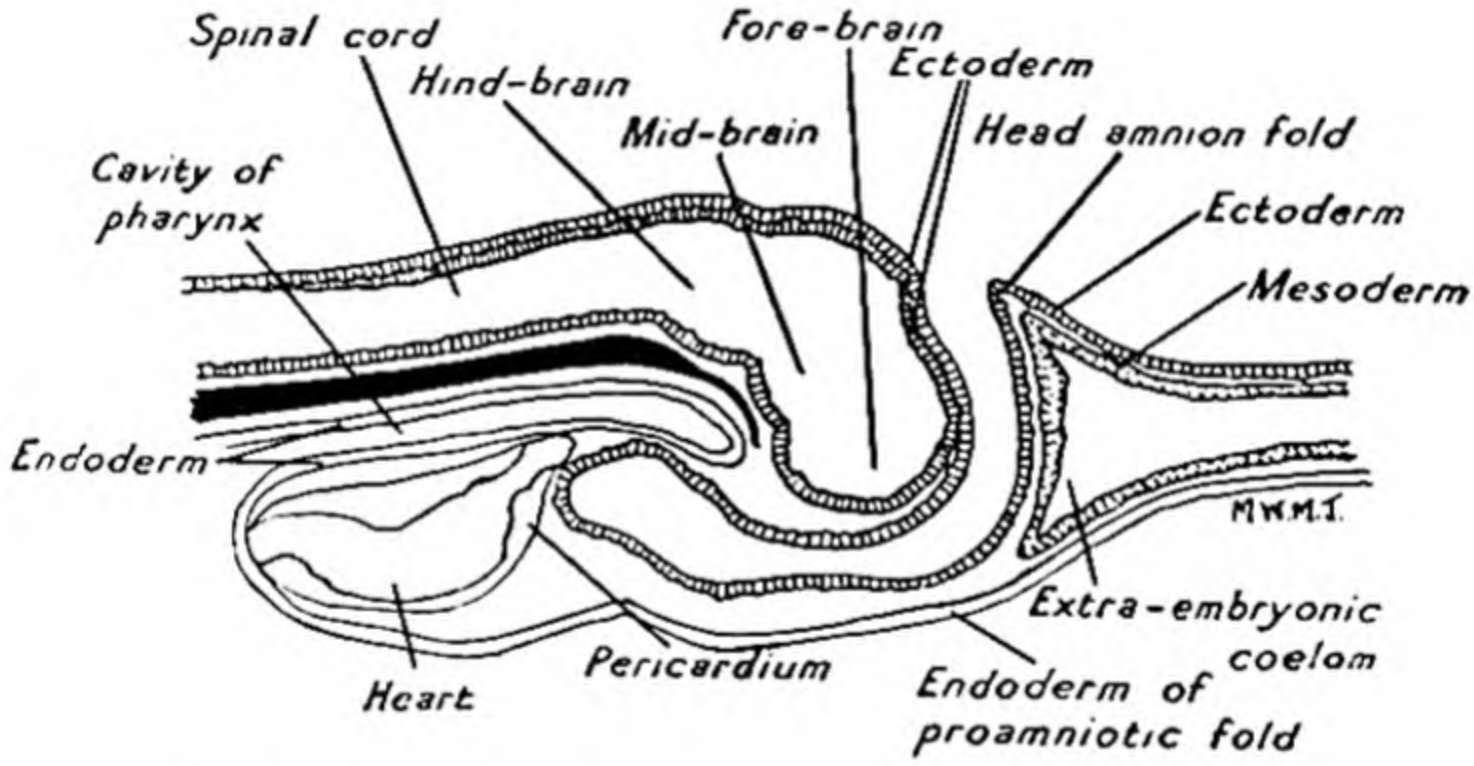


FIG. 311 – *Gallus*. Formation of amnion and head-fold.

thickened, shield-shaped area – the **neural** (or **medullary**) **plate**. As the primitive streak shortens, retreating towards the posterior end, so the posterior end of this plate extends backwards, but its elongation is not completed until after the disappearance of the primitive streak. Soon the edges of the neural plate rise up to form the **neural folds**, whilst the central portion sinks to become the **neural groove**. The folds bend over towards each other and eventually meet to form the neural tube. The extreme lateral portion of each fold gives rise to a **neural crest**, as in the frog. Meanwhile a crescentic area, known as the **sub-cephalic pocket** (or *head-fold*) appears anterior to the head region. After about twenty-four hours' incubation the head is raised above this depression, which is steadily

deepening and extending backwards under the embryo. Simultaneously the neural tube is being formed at the anterior end of the embryo, but at the posterior end it is still only a shallow groove, with the degenerating primitive streak behind it. As the sub-cephalic pocket deepens and extends below the anterior end of the embryo a blind tube is pinched off above the yolk. This is the beginning of the fore-gut, lined with endoderm. The region incorporating the sub-cephalic pocket consists of ecdoderm and endoderm only, mesoderm extending between these layers subsequently. At this stage it is known as the **pro-amnion**. The anterior limit of the opening into the fore-gut from the yolk is known as the *anterior intestinal portal.*

Mesoderm

Between the ectodermal and endodermal layers on either side of the embryonic axis is a sheet of mesodermal cells, extending outwards to the

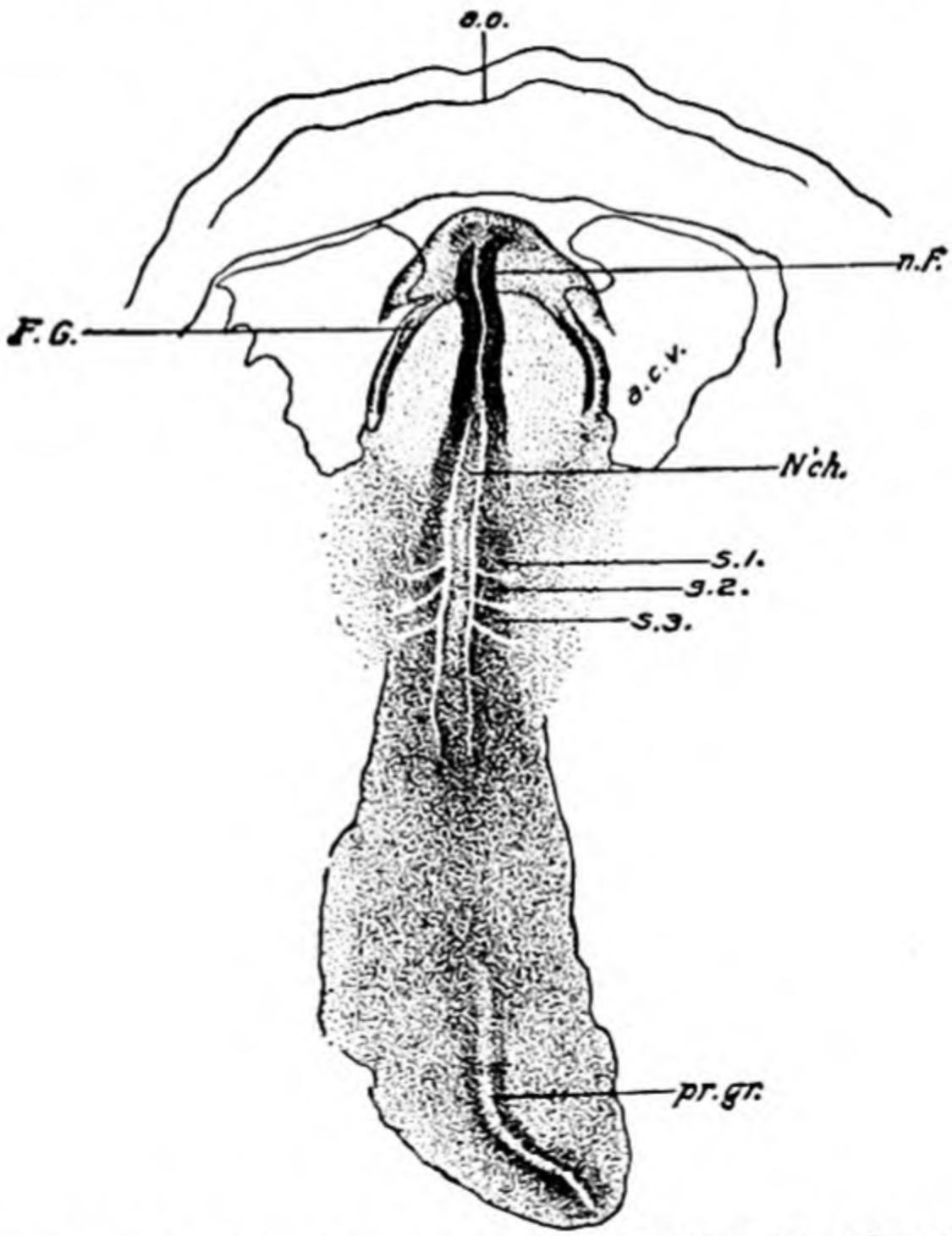


FIG. 312 – *Gallus*. Young embryo. (From Lillie's 'Development of the Chick'. Henry Holt.)
a.o., area opaca, inner margin; *F.G.*, fore-gut; *N'ch.*, notochord; *n.F.*, neural fold; *pr.gr.*, primitive streak; *S.*1, *S.*2, *S.*3, first three mesodermal somites.

margin of the blastoderm. It has been pointed out above that the notochordal process extends forwards in the middle line from the primitive knot. This process provides the first stiffening structure of the embryo, its cells subsequently becoming tightly inflated with fluid and a sheath being secreted about it by the adjacent mesoderm cells. This same notochordal process is also an organiser (page 515), for if it is removed at an early stage the overlying ectoderm fails to develop into a neural tube. While the sub-cephalic pocket is developing the mesoderm on either side of the notochord becomes thickened forming the **paraxial mesoderm**. Soon these masses are dissected by transverse grooves into somites, the first pair appearing at the end of twenty hours' incubation and thereafter one pair being laid down per hour for a while, though the rate is subsequently decreased, until there are some thirty-five in all. Soon myocoels appear, but these are smaller than in the frog and eventually disappear completely. The somites themselves, again as in the frog, are later responsible for the laying down of the vertebrae, the segmental

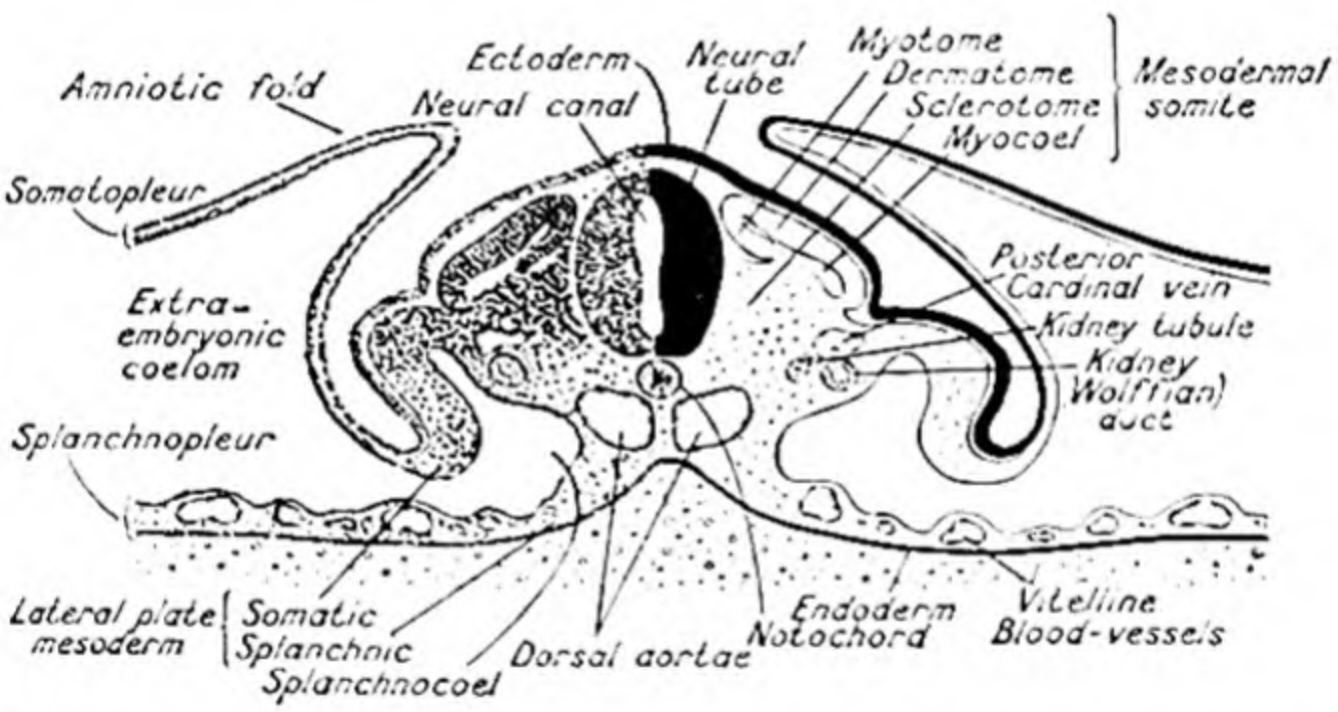


FIG. 313 – Transverse section of embryo, showing origin of amniotic folds.

muscles and the dermis. On either side of the paraxial mesoderm the **lateral plate mesoderm** extends. This is a thin layer, reaching almost to the limits of the blastoderm and remaining unsegmented. Eventually a cavity – the **splanchnocoel** – divides it into an outer **somatic layer** and an inner **splanchnic layer**, as in the frog. Connecting each somite with the lateral plate mesoderm is a narrow tract of cells, constituting the **intermediate cell mass**. Subsequently this becomes segmented, forming **nephrotomes**, the cavities of which are the **nephrocoels**. In this way the foundation of the excretory system is laid down. Along the inner region of the area opaca, cells of the splanchnic mesoderm become aggregated to form blood islands. This region is in consequence now known as the **area vasculosa**. Gradually the islands extend into the

area pellucida, whilst the cell masses become hollow to form red blood-corpuscles and blood-vessels. All the above changes are effected within the first twenty-four hours' incubation.

Embryonic Membranes

As the developing chick embryo increases in size a more generous supply of oxygen and food becomes necessary, together with facilities

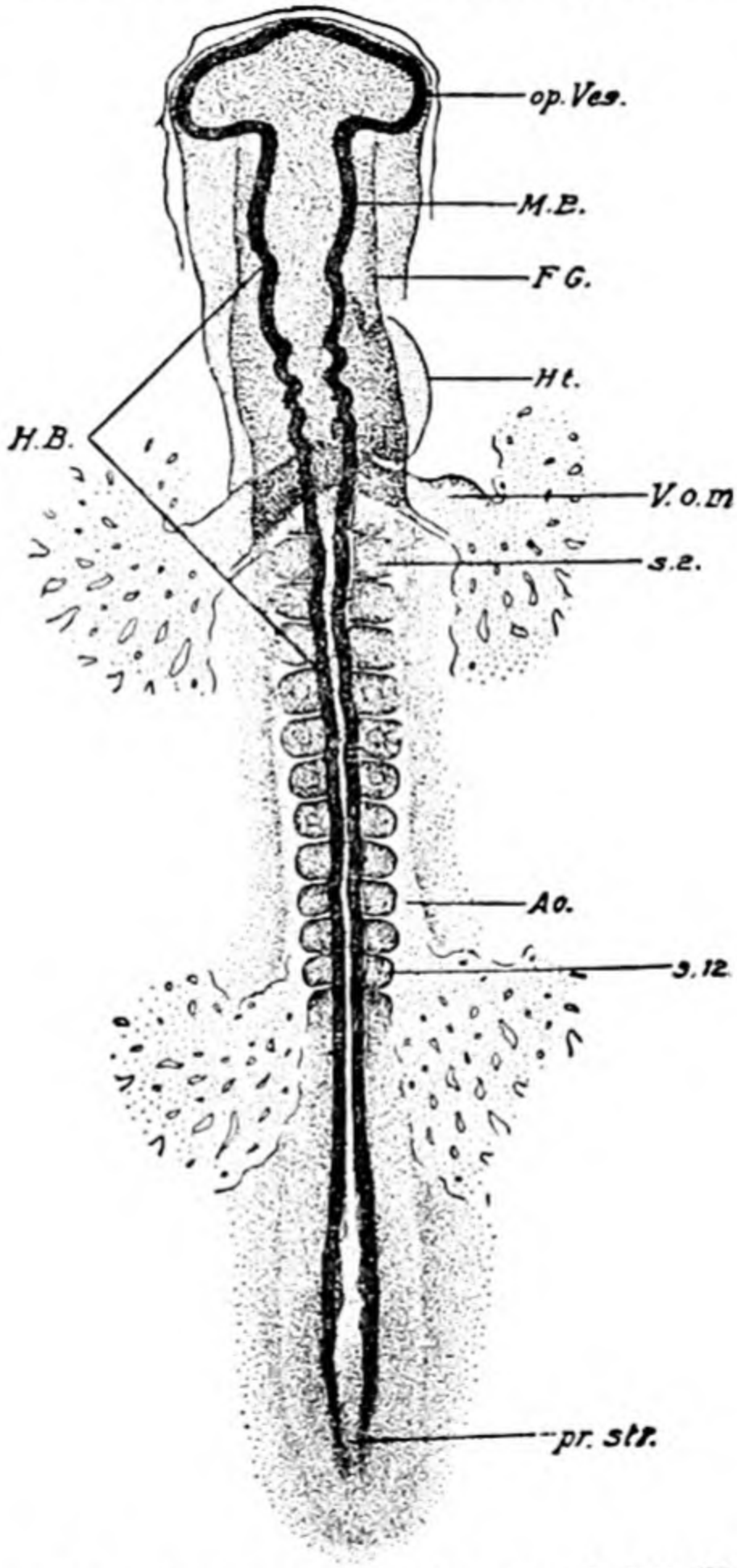


FIG. 314 – *Gallus*. Blastoderm on the second day. (From Lillie's 'Development of the Chick'. Henry Holt.)
Ao., aorta; *F.G.*, fore-gut; *H.B.*, hind-brain; *Ht.*, heart; *op.Ves.*, optic vesicle; *pr.str.*, primitive streak; *S.*2, *S.*12., second and twelfth mesodermal somites; *V.o.m.*, vitelline veins.

for the storage of harmful waste matter, since it cannot diffuse away through the shell and shell membranes. These problems are solved by the development of the embryonic membranes.

AMNION AND CHORION. Due to increasing weight the head sinks down on to the pro-amnion. At about the ten-somite stage a *head amnion fold* begins to elevate itself from the extra-embryonic area in front of the

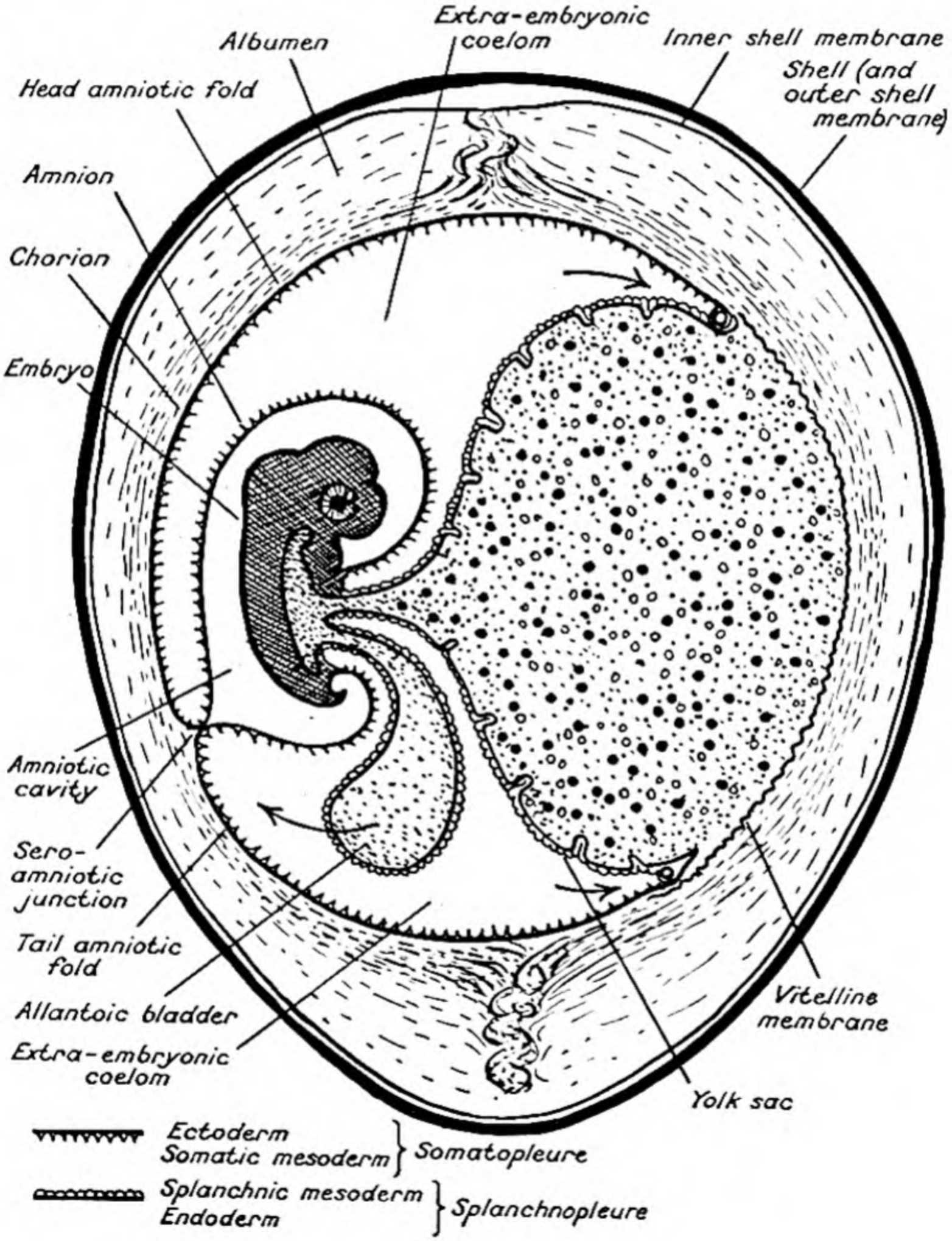


FIG. 315 – *Gallus*. Early stage of development of the embryonic membranes.

head and to extend backwards over the embryo. Later, and in like manner, a *tail amnion fold* arises behind the embryo. From both folds growth now proceeds laterally, and soon the head, tail and lateral folds coalesce completely to roof over the embryo. Each fold involves both ectoderm and mesoderm (somatopleur). The intrusion of extra-embryonic coelom into the folds results in their becoming two-layered, the outer wall constituting the **chorion** and the inner the **amnion**. Between the latter and the embryo is a fluid-filled space – the **amniotic cavity** –

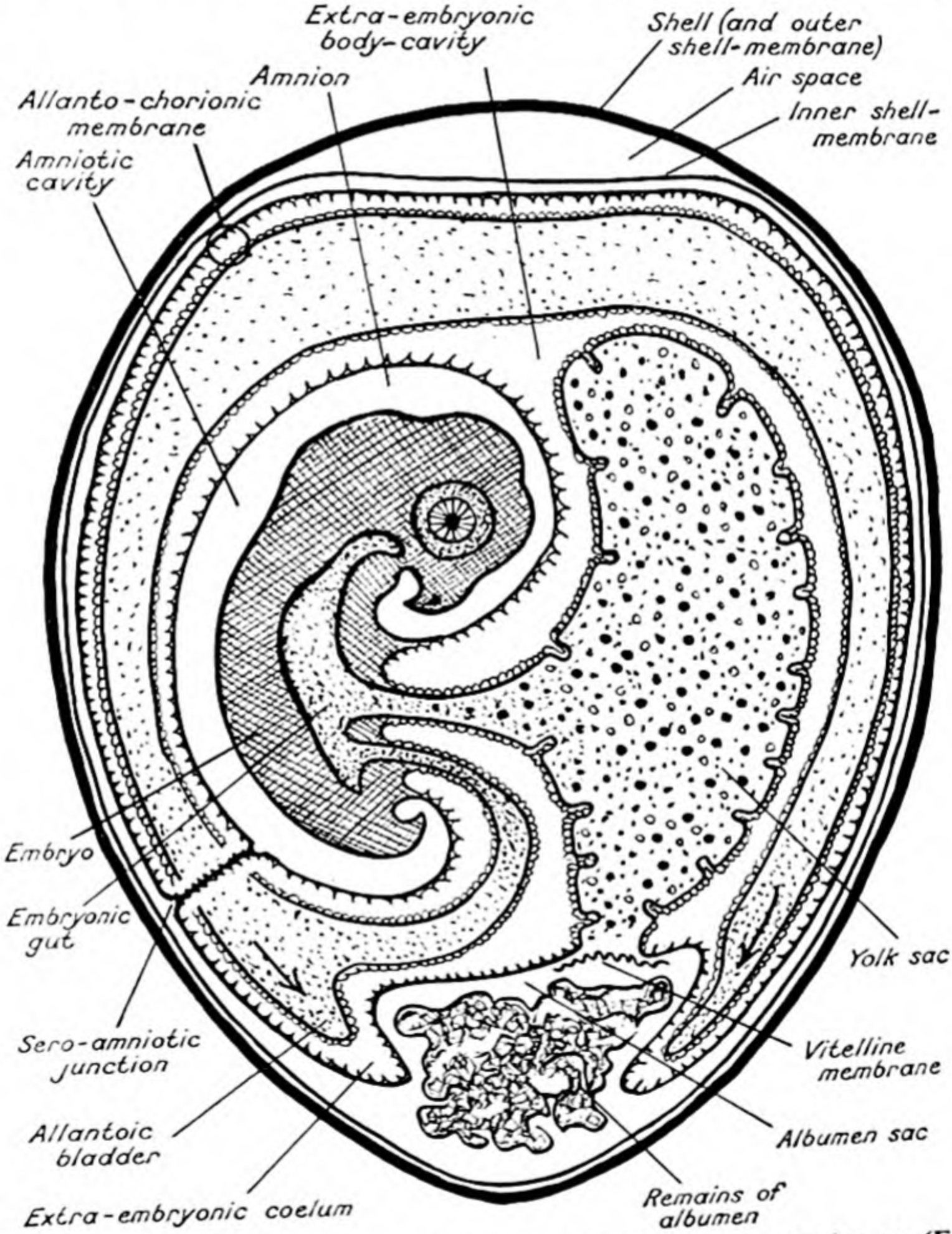


FIG. 316 – *Gallus*. Late stage of development of the embryonic membranes. (For the sake of simplicity the proamnion is omitted.)

protecting the embryo itself from shock, variations in temperature and, above all, desiccation. This development is characteristic of reptiles, birds and mammals, which are therefore collectively classed as the *Amniota*. It is of vital significance in relation to the development of eggs

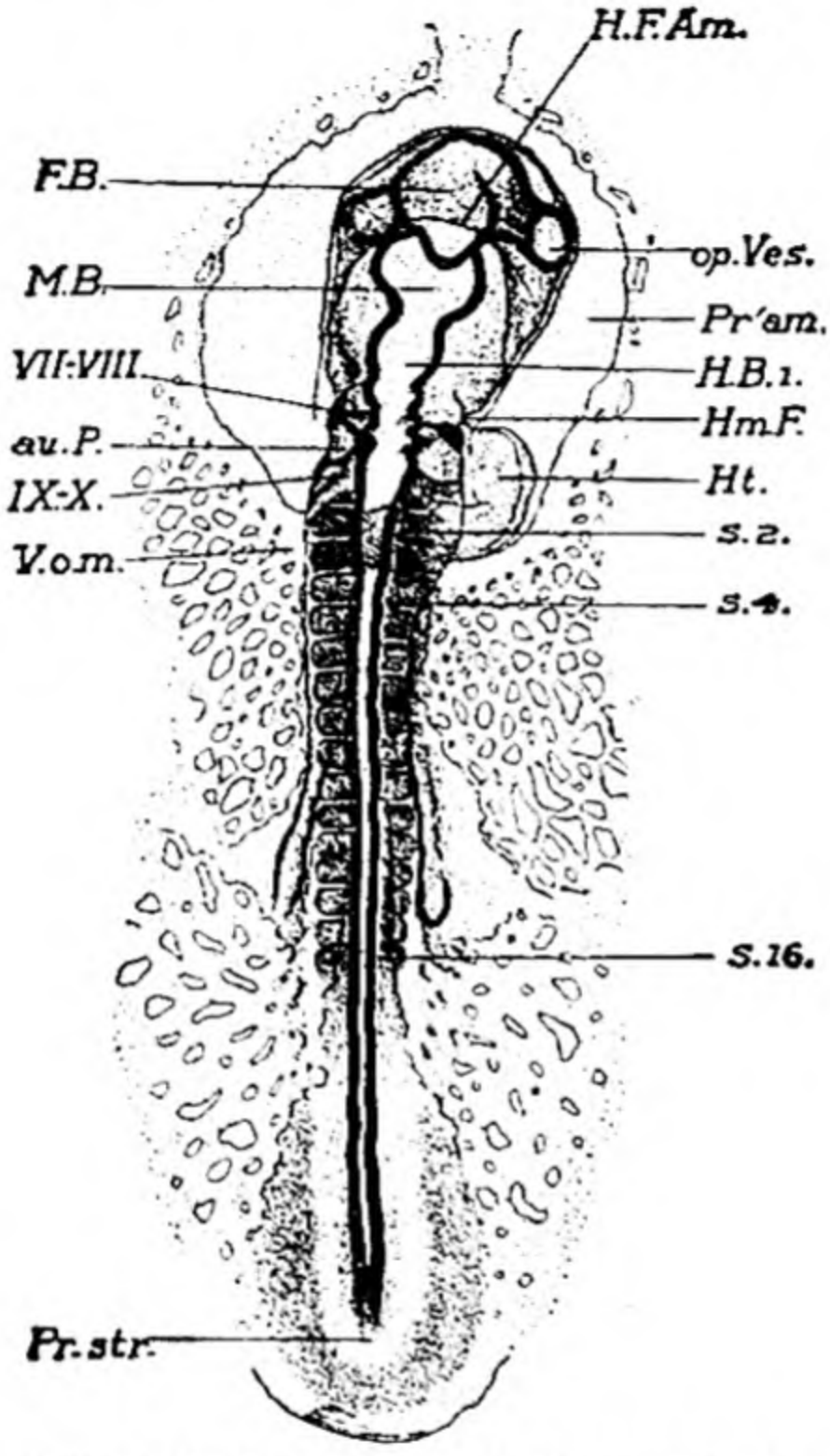


FIG. 317 – *Gallus*. Blastoderm towards the end of the second day. (From Lillie's 'Development of the Chick'. Henry Holt.)
au.P., auditory pit; *F.B.*, fore-brain; *H.B.*1., hind-brain; *H.F.Am.*, head amniotic fold; *Pr'am.*, proamnion; *M.B.*, mid-brain; *op.Ves.*, optic vesicle; *Pr.str.*, primitive streak; *S.*2., S.4, S.16, second, fourth and sixteenth mesodermal somites; *V.o.m.*, vitelline vein; *VII.*, *VIII.*, *IX.*, *X.*, rudiments of 7th, 8th, 9th and 10th cranial nerves.

on land. Fish and Amphibia, on the other hand, being *Anamnia*, are not prejudiced by the absence of such membranes, since their eggs are laid in water. During the subsequent hours of development the trench extends more deeply beneath the embryo until, by the fifth day of incubation, the embryo has been so lifted as to acquire a ventral body-wall and remains connected with the yolk by a short tube – the *yolk stalk*.

YOLK SAC. Endodermal cells of the area opaca gradually extend over the yolk, digesting it and absorbing the products. Initially diffusion is adequate for the transfer of this food to the embryo, but subsequently transportation is effected by the blood-vessels of the area vasculosa. By the end of the sixth day the yolk is almost completely enclosed. Extra-embryonic coelom extends into this covering layer, whilst endodermal processes penetrate the yolk, particles of which are ingested. In this condition the membrane adjacent to the yolk is termed the **yolk sac**, the lining of which is folded so as to increase the surface-area.

ALLANTOIS. This arises as a ventral outpushing from the hind-gut of the embryo and consists of a layer of splanchnic mesoderm, lined with endoderm. It grows rapidly, extending into the extra-embryonic coelom until virtually enveloping the embryo. By the ninth day it fills the coelom and its outer mesodermal covering fuses with that of the overlying chorion to form the *chorio-allantois*. The whole structure becomes highly vascularised and functions as an organ of gaseous exchange, oxygen and carbon dioxide diffusing through the shell and shell membranes. The allantoic and yolk stalks together constitute the *umbilical cord*.

The allantois also serves as a receptacle for metabolic waste from the embryonic kidneys. Uric acid is excreted and crystals of this substance are deposited in the allantois.

ALBUMEN SAC. As development proceeds, water is absorbed from the albumen. Much of this water accumulates beneath the blastoderm and in the amniotic cavity. The albumen becomes very viscous and sinks to the bottom of the egg, where it is enclosed by the folds of the chorio-allantois, constituting the **albumen sac**.

Simultaneously with the above development the anterior end of the tubular nerve-cord has become clearly divided by constrictions into fore-, mid- and hind-brains, whilst rudimentary eyes and ears appear. The development of these organs, largely the same in all vertebrates, is described in some detail on page 542. As already indicated (page 531) the head sinks down into the pro-amniotic area and bends at a point between the fore- and hind-brains. This is the *cranial flexure*. At the same time the head is pushed over to one side, lying with the right side uppermost. This turning movement commences in the neck region and is known as the *cervical flexure*. The movement is continued backwards until the whole embryo lies on its left side.

Vascular System

This is well established by the third day; indeed the heart and pericardium, whose development will first be considered, begin to be formed towards the end of the second day. The coelomic cavities in the region of the future heart are, at this stage, very large and constitute the **amniocardiac vesicles**. The endoderm of the future fore-gut and the splanchnopleur covering it now extend inwards on each side, and the ventral

junction of the two endodermal folds results in the formation of a floor to the pharynx. Before this is completed, however, there appears between the endoderm and its covering splanchnopleur, on each side, a large blood-vessel, continuous posteriorly with the extra-embryonic vessels. Eventually, following the fusion of the endoderm folds, the folds of splanchnic mesoderm also unite ventrally, whilst the two blood-vessels noted above coalesce to form a single longitudinal tube. The wall of this tube constitutes the **endocardium** and gives rise to the lining (endothelium) of the future heart, whilst the layer of splanchnic mesoderm enclosing it as a result of the fusion already alluded to constitutes the **myocardium** and forms the muscular wall of the heart. Reference to Fig. 318 will help

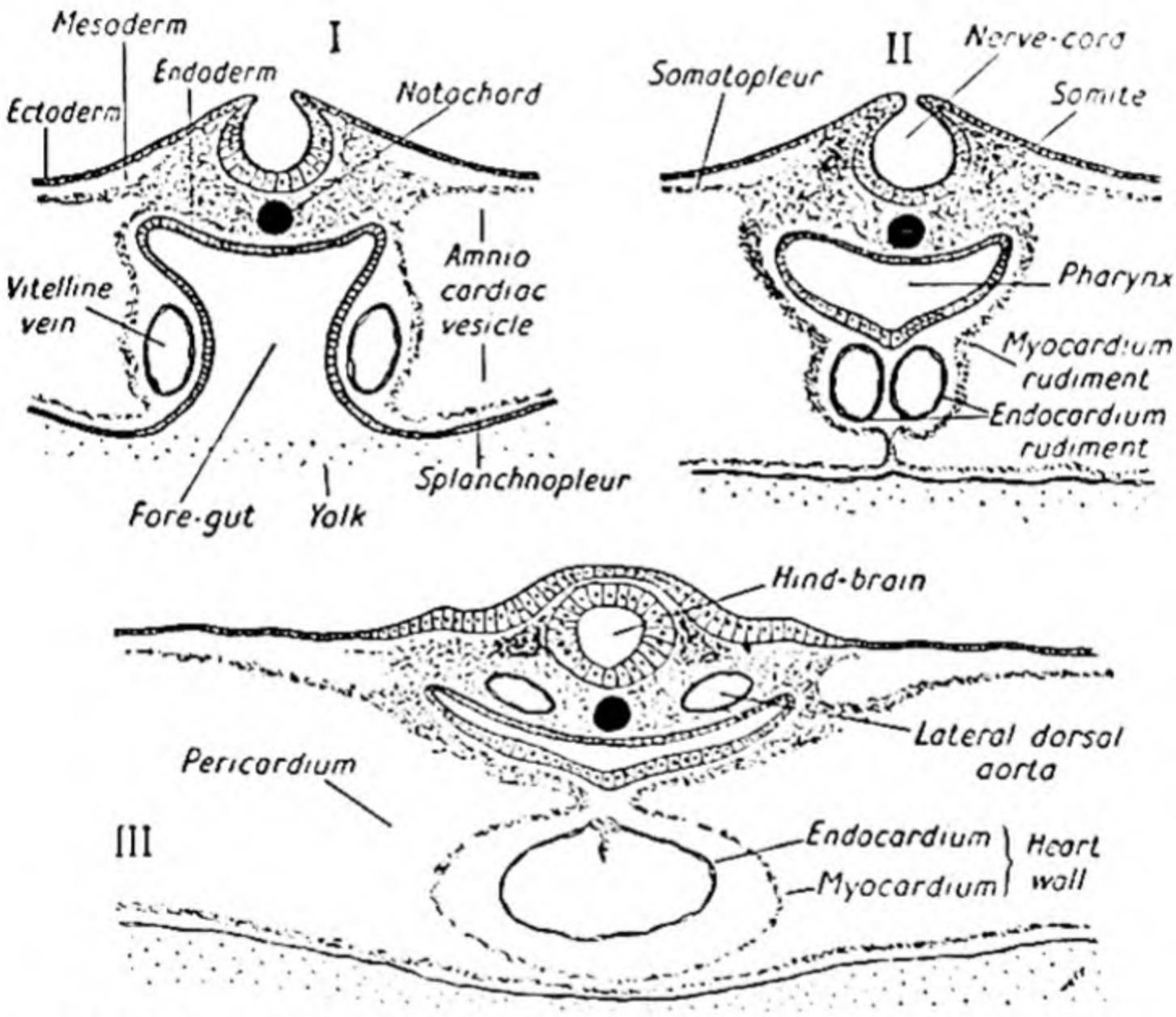


FIG. 318 – Diagram to show the development of the heart and the pericardium in the chick. (After Grove and Newell.)

to make clear the relationships and mode of origin of these components. At the line of junction of the two folds of splanchnic mesoderm both dorsal and ventral mesenteries (**mesocardia**) are at first present, but eventually the ventral one disappears and the dorsal one is represented only by an anterior and a posterior fragment, suspending the heart in the **pericardial cavity** (Fig. 318), which is now continuous from side to side. Ultimately this cavity becomes separated posteriorly from the remainder

of the splanchnocoel by the formation of a **transverse septum**. The heart soon becomes bent upon itself into the characteristic S-shape, and constrictions subdivide it into three primary cavities. Posteriorly is the sinus venosus, receiving blood from the ductus venosus and ductus Cuvieri (see below), and leading forwards to an auricle and thence to a ventricle. Blood is collected up from the area vasculosa into a pair of **anterior vitelline** veins. These unite to form a median **ductus venosus** just in front of the anterior intestinal portal. **Aortic arches** appear, and altogether

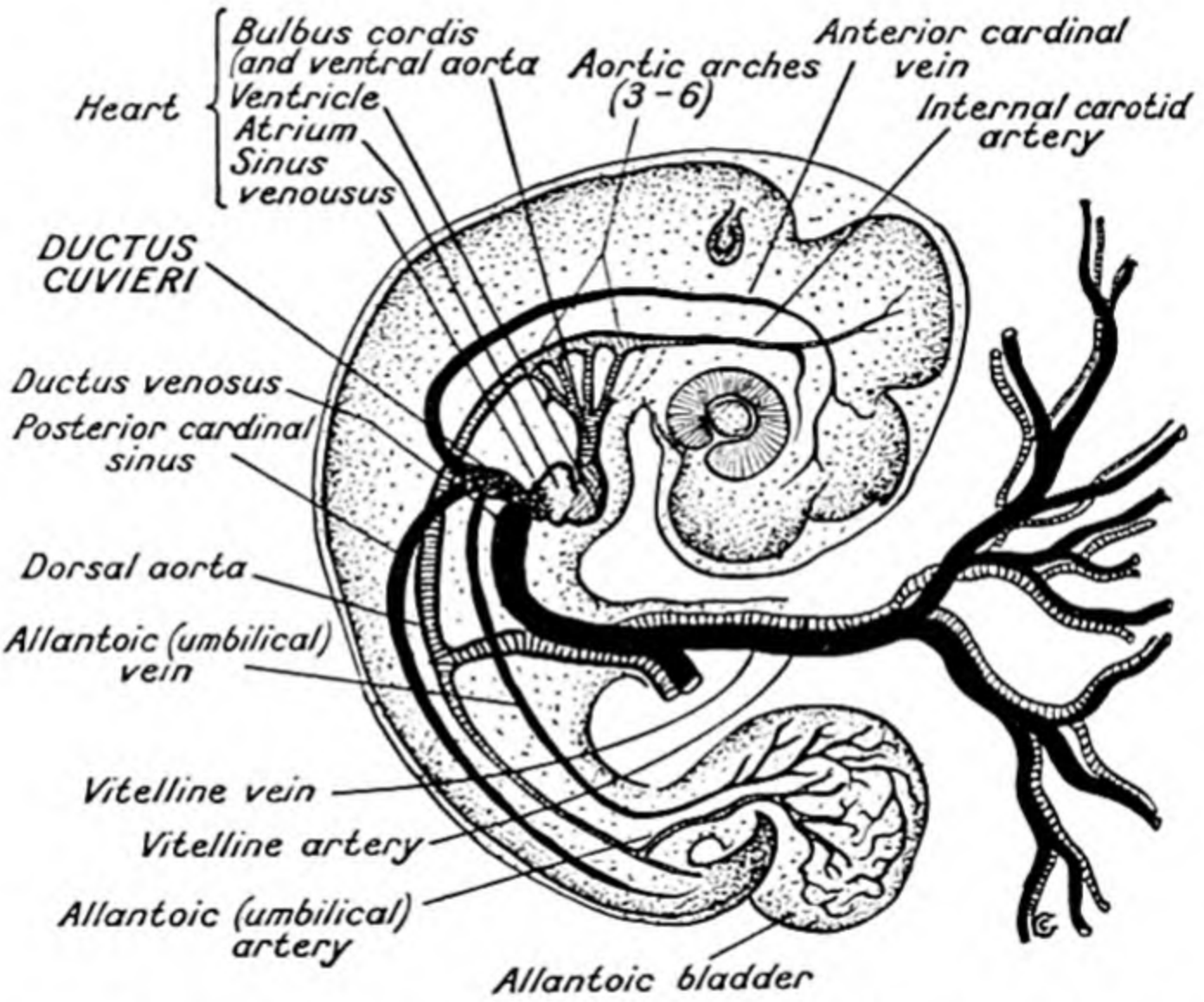


FIG. 319 – *Gallus*. Principal blood-vessels (embryonic and extra-embryonic) of four-day incubated chick.

four pairs of gill-slits are formed, the first (most anterior) three of which became perforated to communicate with the amniotic cavity. The vessels in the visceral arches between these slits communicate on each side with a **lateral dorsal aorta**, which latter structures fuse posteriorly to form a median vessel. This fish-like arrangement does not last long, for the vessel in the fourth visceral arch disappears on the left side, whilst that of the right side becomes the **systemic**. The pair of vessels in the sixth arch give rise to the **pulmonary arteries**, in connexion with the systemic by the **ductus arteriosus**.

Anterior and **posterior cardinal** veins are developed in the body-wall as in the frog, and these reach the heart by the formation of a pair of **ductus Cuvieri** running in the transverse septa, also arising as in *Rana*.

The supply to the allantois is of importance, since this organ functions both for respiration and for excretion. At first blood from this organ is returned by a pair of **umbilical** veins to the ductus Cuvieri of each side. Later the right one degenerates and the left one opens direct into the ductus venosus. When septa have been laid down to divide the heart into right and left auricles and ventricles this blood comes to run into the right auricle, whilst **pulmonary** veins are developed, connecting the lungs with the left auricle. But at this stage these organs are not yet functional, and the septum between the auricles breaks down to permit the passage of oxygenated blood direct to the left side of the heart. Blood which leaves the right ventricle would normally go to the lungs, but this is avoided by means of the ductus arteriosus, so that for the time being all blood leaving the heart reaches the systemic arch. Only at hatching is the inter-auricular septum again completed.

Kidneys

The pronephros and mesonephros develop as in the frog, but they are later replaced by the adult kidney, the **metanephros**. This is formed posterior to the mesonephros from the nephrotomes of that region, known collectively as the **metanephrogenous tissue**. The **ureter**, by which urine is passed to the cloaca, arises from the base of the Wolffian duct. It grows forwards, and branches to form collecting tubules which penetrate the metanephros. The kidney itself is richly vascularised and Bowman's capsules, each containing a glomerulus, are formed as in the frog.

The original Wolffian duct is conserved in the male as a vas deferens for the conveyance of sperm to the cloaca. A Müllerian duct is developed in both sexes from coelomic epithelium, a plate of this tissue becoming closed over to form a tube after the manner in which the nerve-cord is developed. Both these ducts later disappear in the male, whilst in the female the left one alone remains as the oviduct, since there is no right ovary in birds.

Hatching

Immediately prior to hatching, with the embryo lying on its left side and with its head directed towards the blunt end of the egg, the beak is used to pierce the inner shell membrane, thus enabling the chick to draw air from the air chamber into its lungs. The ductus arteriosus closes, with the result that more blood circulates through the lungs. The beak is now armed with a pointed projection, termed the *egg tooth*, with which the shell is pierced. Connexion with the allantois is severed, whilst by this time the yolk sac has been absorbed, so that the chick now emerges, free from all the accessory structures which have been so important during the process of development.

ORYCTOLAGUS

In conclusion, the chief stages in the development of *Oryctolagus* will be considered, largely in comparison with parallel processes in forms previously described.

Fertilisation

The egg of the rabbit is very small (0.12 mm. in diameter), containing little or no yolk. It is released from its Graafian follicle (page 346) enclosed in a striated zona radiata secreted by the ovary, the first polar body having already been extruded. The egg is fertilised in the Fallopian tube, both head and tail of the sperm penetrating the cytoplasm. The tail, however, soon disappears, whilst immediately after the entry of the sperm the second polar body is extruded.

Cleavage

Unlike the egg of the chick, cleavage of the mammalian egg is total, or holoblastic. In accordance with the evolutionary descent of the Mammalia from reptiles, whose eggs were yolky, their development more closely resembles that of birds than it does that of *Branchiostoma*, despite the almost complete absence of yolk. By total cleavage a solid ball of cells, known as a **morula**, is formed. As this passes down the oviduct a layer of albumen is secreted about it. At the same time a small cavity appears as a result of the separation of cells, and this enlarges, the wall enclosing the cavity being one cell thick except on one side, where an aggregation of cells, known as the **inner cell mass**, occurs. The wall of this structure is termed the **trophoblast**, whilst the entire embryo at this stage is a **blastocyst**. In this condition the blastocyst becomes attached to the wall of the uterus, the process being known as **implantation**, or **nidation**. Passage from upper oviduct to uterus takes place during cleavage, occupying three or four days in most mammals. The blastocyst remains free in the uterus for variable periods – in the rabbit for four days, in man for six days and in the badger and stoat for some months. Badgers mate in August, but nidation does not take place until early in the following year. Much research into the mechanism of nidation has been undertaken and is still continuing. Nidation consists of the fusion of the foetal membrane with the uterine mucosa in order to allow physiological exchange. It is prefaced by the development of the *decidua* – the maternal component of the placenta (page 543). This is marked by the accumulation of polysaccharides, vitamins and enzymes in the uterine tissue, together with greatly increased local vascularisation. It has been conclusively demonstrated that histamine, released from the mast cells of the uterine wall under the influence of oestrogen, is responsible for decidualiastion (development of the decidua), but that histamine alone will not induce nidation of the blastocyst. A second and synchronised process must, therefore, occur. The mechanism is believed to be some-

what as follows. Progesterone from the corpus luteum is responsible for the general physiology of the genital tract, for cleavage and for the migration of the blastocyst. At a specific point in time there occurs what is termed an 'oestrogen surge', related to the normal oestrous cycle of the species. This oestrogen is derived either from the ovary or from the blastocyst (or its membranes). In the case of the rabbit it is more likely to be the latter, since ovulation occurs after coitus. The oestrogen surge affects the blastocyst-uterine endometrial complex, activating the blastocyst for nidation. Histamine liberation follows and stimulates decidualisation, involving lysis (page 357) and division and transformation of the tissues of the endometrium.

Further information on this interesting topic will be found in an article by Dr M. C. Shelesnyak in *Endeavour*, Vol. XIX, No. 74 (I.C.I.).

Formation of Germ-layers

The inner cell mass becomes flattened beneath the trophoblast to form the **embryonic plate**, whilst its innermost layer becomes extended to form a lining to the trophoblast. This new layer is the hypoblast, whilst the cavity which it encloses represents the yolk-sac. The trophoblast cells immediately above the embryonic plate are known as the **cells of Rauber**,

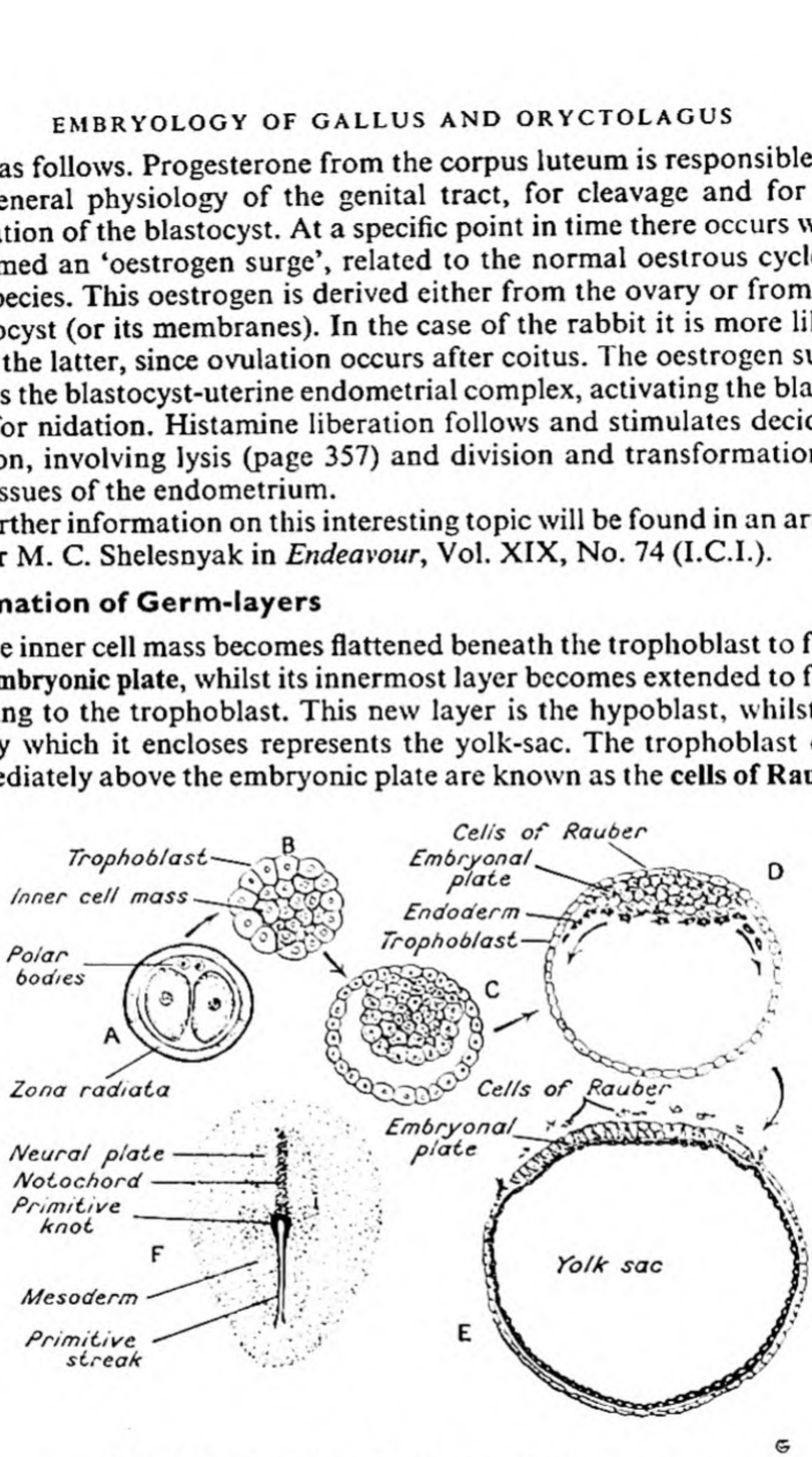


FIG. 320 – *Oryctolagus*. Early stages in development.
A., Two-cell stage; *B*., Morula stage; *C*., Early blastocyst; *D*., Later blastocyst, showing flattening of embryonal knob and formation of endoderm; *E*., Embryonal plate exposed by loss of cells of Rauber; *F*., Surface view of embryonal plate, showing primitive streak. In *B*, *C*, *D* and *E* the zona radiata has been omitted.

and they disappear, leaving the embryonic plate exposed on the surface. Some of the **mesoderm** is formed by extension between the hyphoblast and epiblast (trophoblast) of cells proliferated by the middle layers of the inner cell mass. A **primitive streak** is formed along the middle line of the embryonic plate, as in the chick, and from this is derived the remainder of the mesoderm. The notochord is formed, as in the chick, by the proliferation of cells forwards between the epiblast and the hypoblast from the primitive knot – i.e. the 'dorsal lip' portion of the primitive streak, which, as a result, appears to move backwards. Mesoderm extends forwards on either side of the notochord. A **nerve-cord** is formed as in other types by the raising of **neural folds**, whilst the appearance of head- and tail-folds causes the front and hind ends of the embryo to be raised from the extra-embryonic tissue. In this way a floor is formed to the extremities of the gut, whilst anterior and posterior intestinal portals arise.

To cope with the increasing nutritional needs of the embryo outgrowths (*villi*) from the trophoblast penetrate into the wall of the uterus making implantation more secure. This structure is, however, only temporary and is soon replaced by a more efficient organ – the true placenta (page 541).

Amnion

The amnion, as in the chick, is formed from extra-embryonic ecto-

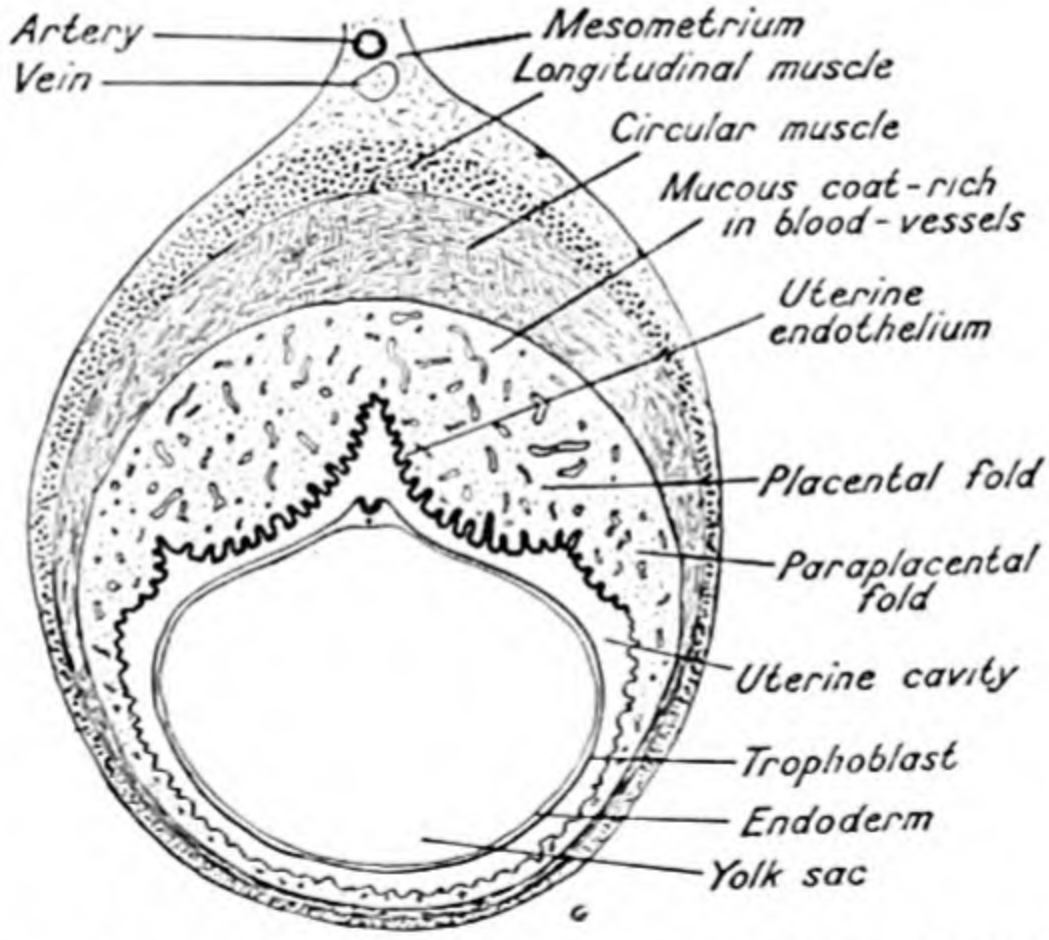


FIG. 321 – *Oryctolagus*. Transverse section of uterus, containing blastocyst (7–8 days); embryo lies free in uterine cavity, with germinal area opposite mesometrium and placental folds; uterine tissues hypertrophy on mesometrial side. (Modified from Eales – *Practical Histology and Embryology*.)

derm (trophoblast). Two folds, one anterior and one posterior, arise from the edge of the embryonic plate, and soon the embryo becomes completely enclosed within an amniotic cavity. Thus the trophoblast of *Oryctolagus* corresponds closely to the chorion of *Gallus*.

Coelom

As in the chick a split occurs in the mesoderm, so that a coelom is formed, bordered by an inner (splanchnic) and outer (somatic) layer of mesoderm. The extra-embryonic region of the somatic layer extends

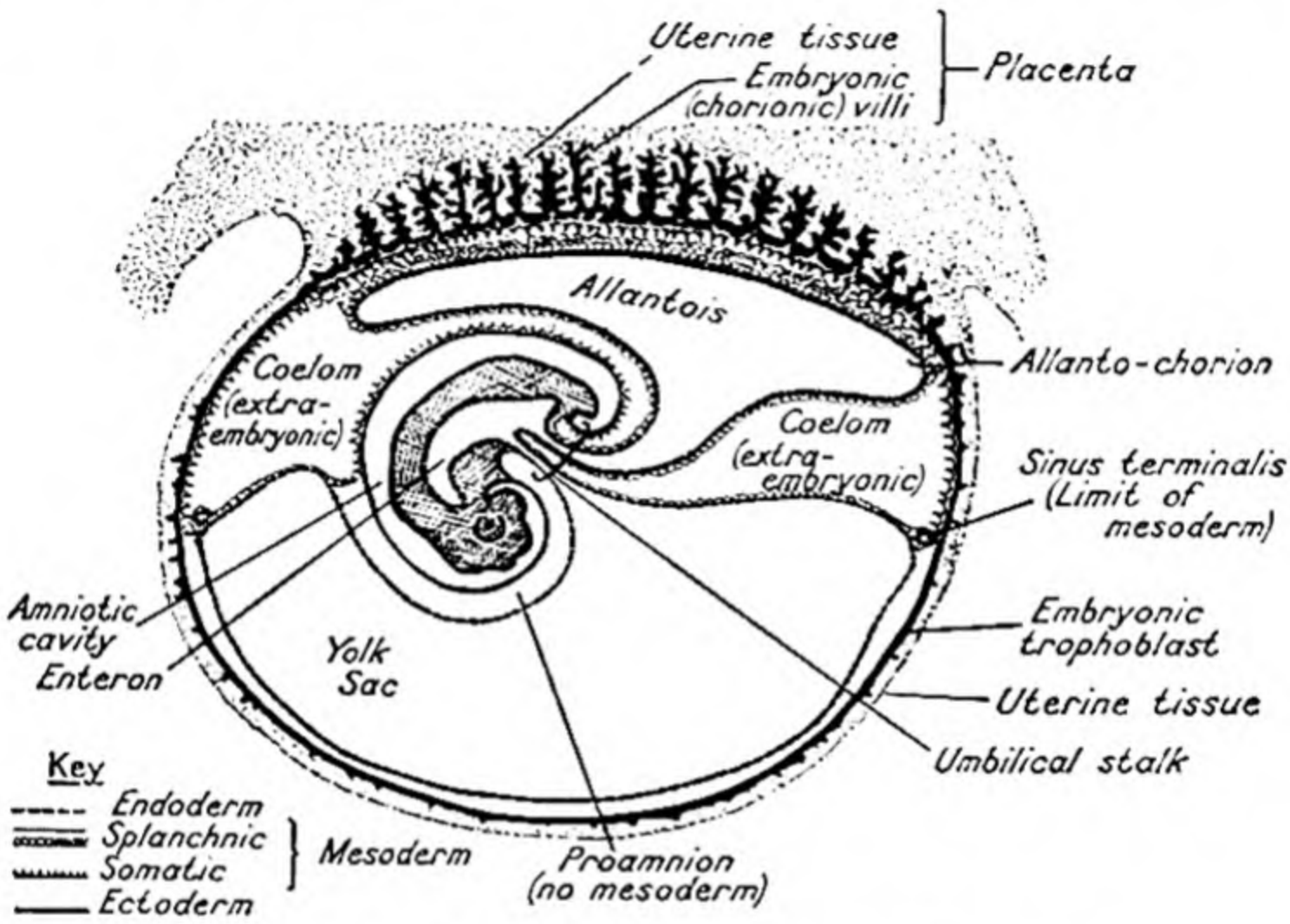


FIG. 322 – Foetal membranes and placenta of a mammal.

around the amnion, separating it from the trophoblast (chorion). Mesoderm does not extend far around the yolk-sac, and eventually the lower wall of the yolk-sac disappears completely, so that it opens direct into the cavity of the uterus.

Placenta

The **allantois**, as in the chick, arises as a diverticulum of the hind-gut and grows up around the embryo, pushing into the extra-embryonic body-cavity and carrying with it a layer of splanchnic mesoderm, which by now contains blood-vessels. This mesoderm fuses with the somatic mesoderm underlying the trophoblast (chorion) in the latter's region of contact with the uterine wall, whilst the allantoic blood-vessels penetrate the trophoblast. In this way the **allantoic placenta** is formed. Whereas in the chick the allantois is a respiratory organ, in the rabbit it serves to

place the embryo in nutritive connexion with the mother, as well as facilitating embryonic respiration and excretion. Contact is made more intimate by the disappearance, in the placental region, of the connective tissue and endothelium of the uterine wall, as well as the endothelium of the blood-vessels. whilst the trophoblast and uterine wall become thick and contain many lacunae. The umbilical artery and vein are the blood-vessels of the allantois. They are enclosed by the *umbilical cord*, which is itself formed from the base of the amnion, growing backwards along the neck of the allantois. Thus nutritive substances and oxygen pass from mother to embryo, though the two blood-streams are never in continuity. That this is so may clearly be determined by the fact that the erythrocytes of the foetus are nucleate. Excretory products, including carbon dioxide, from the embryo are eliminated via the maternal circulation. The form of the placenta is somewhat variable. In the pig, for example, the wrinkled outer surface of the chorion lies closely adpressed to the grooved uterine wall, there being no erosion of the maternal tissues. At birth only the foetal portion of the placenta comes away, there being no loss of uterine tissue. Such a placenta is described as *non-deciduate*. Most mammals possess a *deciduate* placenta and at birth part of the lining of the uterus is torn away.

Development of the Eye

This begins early, soon after the closure of the neural folds to form the rudimentary nerve-cord. A pair of diverticula arise ventro-laterally from the fore-brain to form the **primary optic vesicles**. Their bases become constricted, thus forming the **optic stalk** associated with each vesicle. At the same time a localised thickening of the embryonic ectoderm immediately opposite each optic vesicle gives the first indication of the formation of a lens. Each optic vesicle now becomes invaginated opposite the rudimentary lens, thus giving rise to the **secondary optic vesicle**, or **optic cup**, which is thus a double-layered structure. The retina is formed by the further development of *both* of these layers. The wall lining the new cavity thus created becomes differentiated into two further layers; that immediately adjacent to the cavity of the optic cup gives rise to nerve-cells, whilst the more superficial layer comes to consist largely of rods and cones. The covering layer of the cup – i.e. the layer which has not been invaginated – forms the pigmented layer, or fringe, of the retina. Meanwhile the formation of the lens has been completed by further ectodermal thickening and invagination and eventual separation inwards. It now consists largely of meridional, transparent, refractive fibres, formed from ectodermal cells, and retains a small cavity. The reconstituted ectoderm opposite to it becomes the conjunctiva. At this stage the pigmented layer of the retina reaches the rim of the optic cup, giving the characteristic colour to the iris, whilst the restricted aperture of the cup is known as the pupil.

Mesenchyme meanwhile has invaded the head and come to enclose the optic vesicles, as shown in Fig. 323. It becomes differentiated primarily into two layers, which eventually constitute the sclerotic (including the cornea) and choroid coats respectively. The six eye-muscles associated with each eye represent the segmental muscles of the first three head somites. The fibres of the optic nerve, arising from the immediate lining of the cavity of the optic cup, elongate and con-

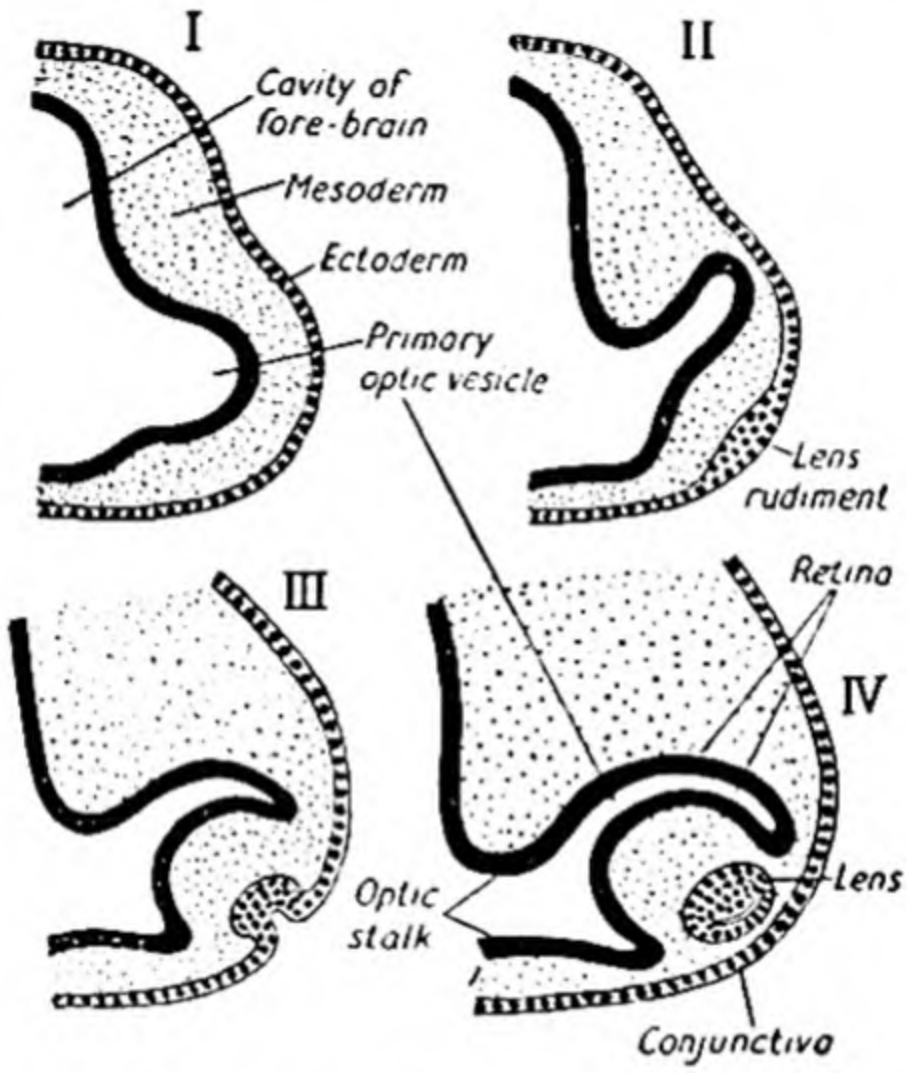


FIG. 323 – Diagrams to show the development of the vertebrate eye, as seen in vertical sections through the embryo head. (After Grove and Newell.)

verge upon the optic stalk, along which they pass to reach the brain. In most vertebrates most of the fibres decussate (cross-over) beneath the floor of the fore-brain, forming the optic chiasma, but in the primates only about half of them do so.

The retina, whose development has been described, is said to be 'inverted', indicating that the rays of light must pass the conducting elements (nerve-fibres) before reaching the sensitive cells, a state of affairs sharply contrasted with that operating in other sense-organs. This is explicable when it is realised that in the original neural plate the sensitive cells are superficial and the conducting elements deeper. Thus when the neural tube is formed the sensitive cells must immediately line its cavity. When the optic vesicle is evaginated, therefore, the conducting cells must be nearer the surface of the skin. The subsequent invagination of the cup

at its distal extremity does nothing to modify this arrangement. This will be made clear by reference to the sequence of events depicted in Fig. 324.

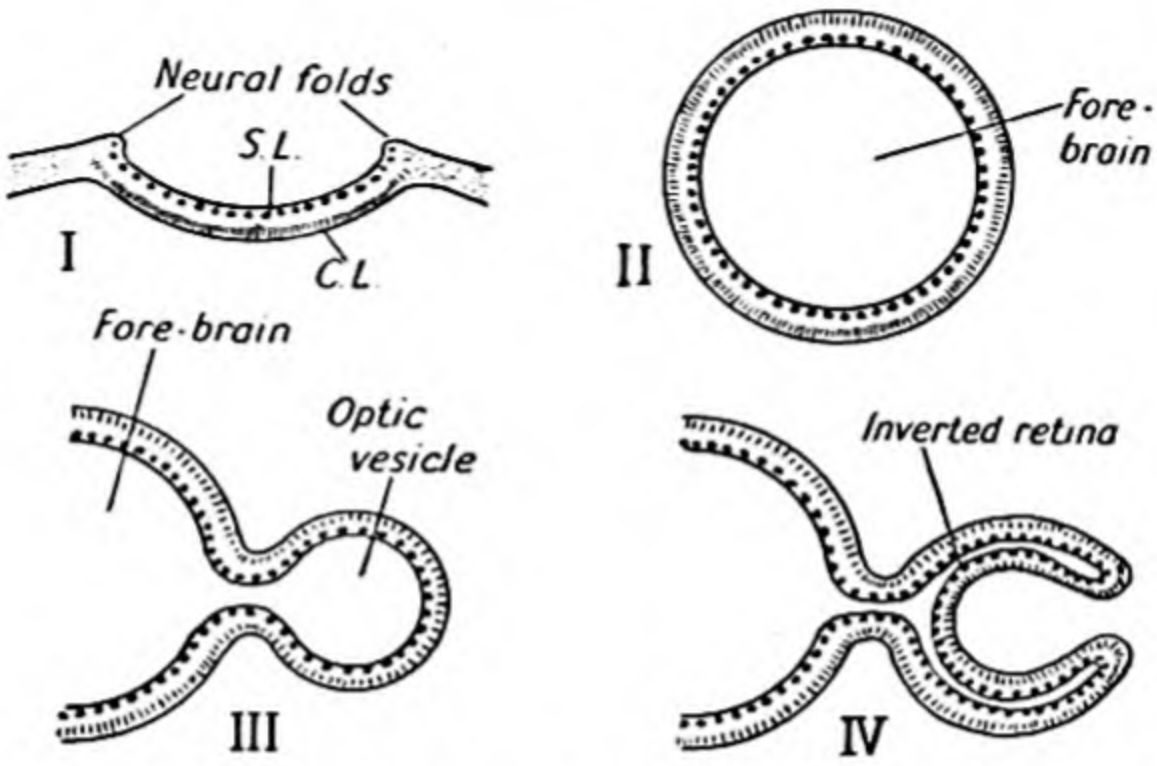


FIG. 324 – Diagrams to show the origin of an inverted retina. *C.L.*, Conducting layer; *S.L.*, Sensitive layer.

When studying this figure it is important to realise that the whole extent of the optic stalk and cup does not become differentiated into sensitive and conducting layers, but continuity is maintained in the diagram in order to make clear the inevitable state of affairs in the lining layer of the retina.

Development of the Ear

In all essentials the development of the ear follows a similar course throughout the Vertebrata. The thickening of a small patch of superficial ectoderm opposite the hind-brain indicates the inception of the formation of the membranous labyrinth. This subsequently sinks inwards and eventually loses connexion with the exterior, forming the **auditory vesicle**. In some forms this vesicle arises from only the inner layers of the ectoderm, in which case it never communicates with the exterior. The ductus endolymphaticus is usually formed as a tubular diverticulum of the auditory vesicle, and in the dogfish, for example, this ductus remains as the narrow tube connecting the vesicle with the exterior. The auditory vesicle soon becomes constricted to form a dorsal utriculus and a ventral sacculus, the ductus endolymphaticus communicating with the latter. Each of the three sem-circular canals is formed by constriction from the utriculus, forming first a tubular structure, which subsequently elongates and becomes characteristically looped. The cochlea arises as a spiral diverticulum from the ventral extremity of the sacculus.

The hyoidean visceral pouch of the fish becomes modified to form the

middle ear and the Eustachian tube of the Tetrapoda. A dorsal expansion of the pouch forms the middle ear and its outer wall fuses with the superficial skin of the head to form the tympanum.

The ear-ossicles vary from group to group. The single columella auris of the frog is the result of the modification of the hyomandibula of the

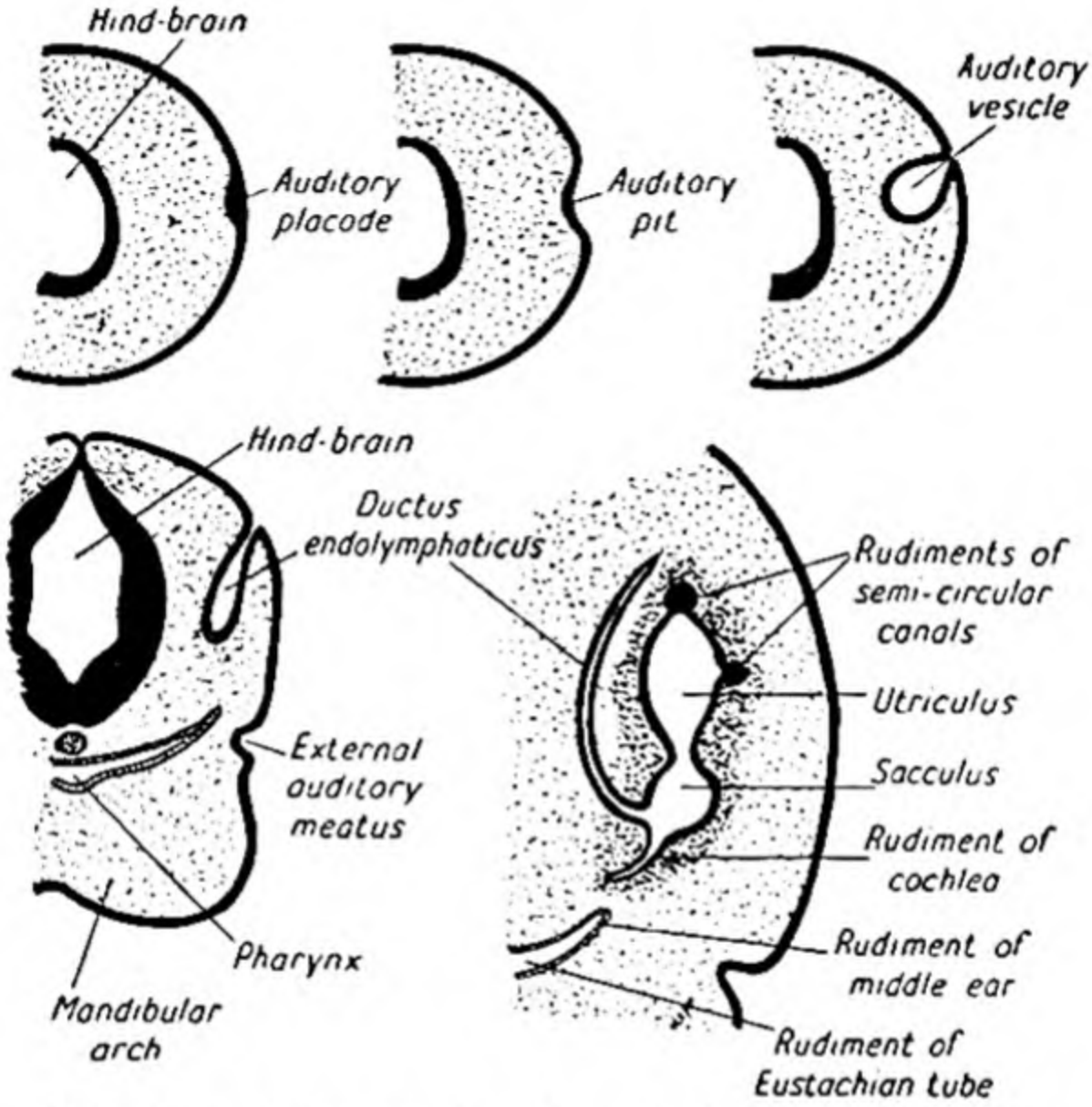


FIG. 325 – Diagrams to show the development of the vertebrate ear, as seen in transverse sections through the embryo head in the region of the hind-brain. (After Grove and Newell.)

fish (page 88), and it remains in the mammal to be represented by the stapes. The malleus and incus have arisen by the positional modification of the articular and quadrate of the reptilian ancestors of the mammals, bones formerly associated with the articulation of the upper and lower jaws. The tympanic bone, which is ring-like and supports the tympanum, has arisen from the angular of lower forms. The auditory capsule itself, composed of cartilage-bone, is derived from the head mesoderm.

Completion of Development

In other respects the development of the rabbit is similar in principle to that of the chick, making allowance for the final differences in adult structure. Thus the final stages in the development of the blood-systems are dissimilar, in accordance with the differences discussed on page 609.

Both ovaries persist in the female, whilst in the male each testis eventually descends into a scrotum. The whole of the enormous increase in size of the embryo is accommodated by the extension of the uterine wall. This is effected by the expansion of the muscle-cells, and not by their increase in number, so that after birth the uterus may regain its original size.

Ossification

There is one event which occurs during the development of all the Craniata except the cartilaginous fish, and that is the process of the

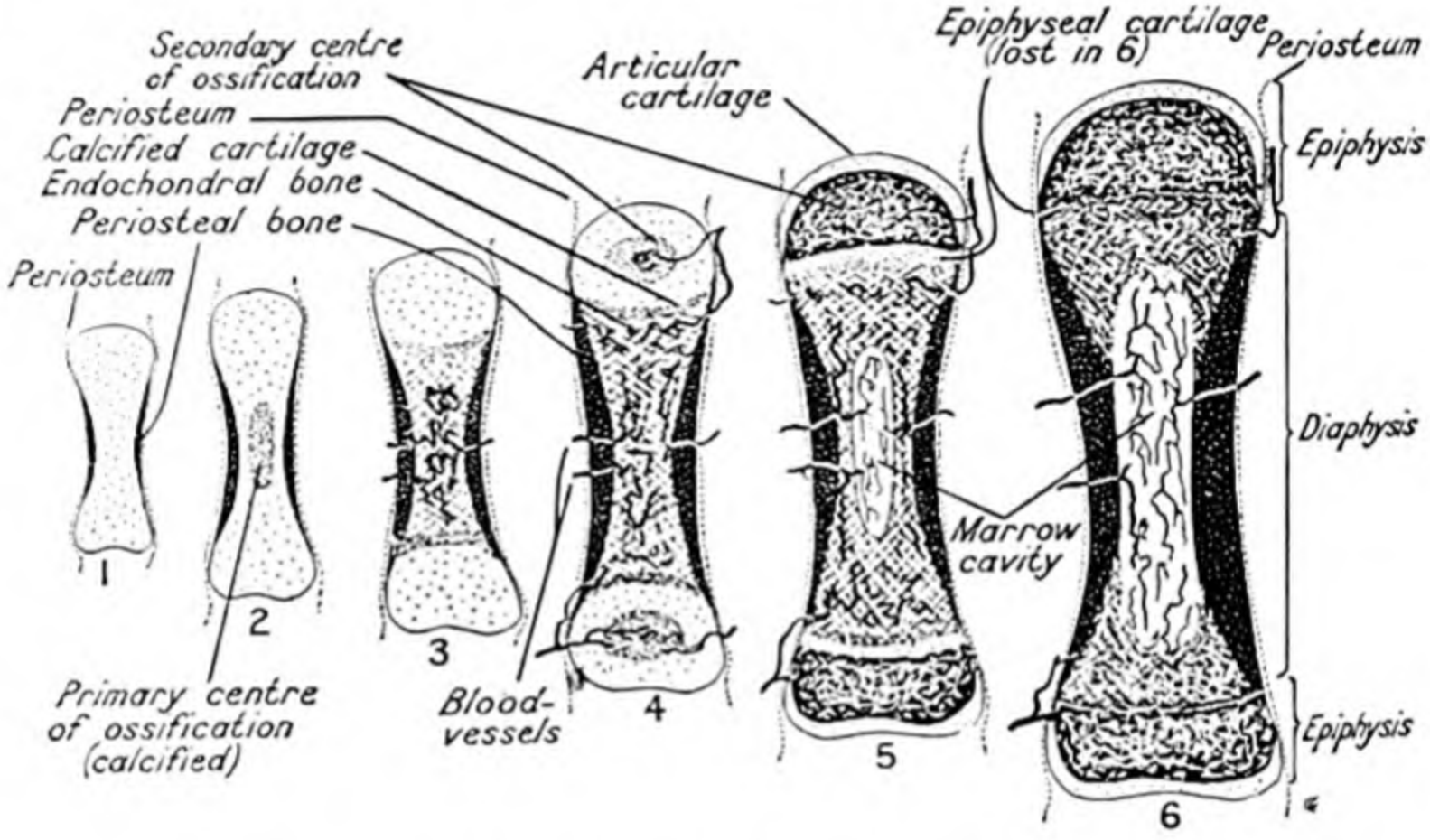


FIG. 326 – Ossification of a long bone. 1., Cartilage, showing the beginning of periosteal bone formation. 2., Commencement of primary centre of ossification within a cartilge (i.e. endochondral); matrix becomes calcified and later eroded by osteoclasts. 3., Area of ossification spreads through activity of osteoblasts. 4., Secondary centres of ossification appear at either end, spreading in 5, where marrow cavity appears through erosion by osteoclasts. 6., Fusion of epiphyses to diaphysis, preventing further growth in length; marrow cavity enlarged and continued spread of periosteal bone.

formation of bone. The structure of this skeletal tissue has already been described (page 326), and it is important to understand the way in which the cells and the matrix have become so characteristically disposed. The process must be considered separately in relation to membrane-bones and cartilage-bones respectively. The latter are so called because they are preformed in cartilage, which is later displaced, whilst the former are laid down directly.

(A) CARTILAGE-BONES. At first there is considerable multiplication of the cartilage-corpuscles, which now become arranged in columns, whilst the matrix undergoes calcification. The original membrane enclosing the cartilage, known as the *perichondrium*, is from this point

onwards termed the **periosteum**, itself divisible into an outer layer of connective tissue, blood-vessels and nerves and an inner layer of fibres, fibroblasts and osteoblasts. The formation of true bone may now be held to commence. The calcified cartilage becomes invaded by connective tissue corpuscles, known as **osteoclasts**. These make their way to the centre and effect erosion of the cartilage towards the surface. They are followed by a second series of superficially similar cells, termed **osteoblasts**. These lay down inter-connected bars of bony tissue, known as **trabeculae**, the spaces between the bars, themselves parallel to the axis of the bone, being filled with blood-vessels and connective tissue cells. Such ossification, proceeding from the centre, is described as **endochondral**. Meanwhile, a much harder layer of bone is being laid down beneath the periosteum, and this is at first dense. By the activities of osteoclasts, spaces – Haversian canals – are formed, and re-modelling by the osteoclasts and osteoblasts results in the final appearance of the bone, of such characteristic structure. Eventually the endochondral bone is similarly re-modelled by these same types of cell, whilst in limb bones the destruction (by osteoclasts) of the central endochondral bone gives rise to the marrow cavity.

In limb bones growth in length is facilitated by the persistance of a disc of cartilage between the shaft diaphysis and epiphysis, and this becomes ossified only when growth is completed.

(B) MEMBRANE-BONES. The position of future membrane-bones is first denoted by the presence of sheets of unspecialised connective tissue cells. These cells lay down a fibrous matrix, subsequently strengthened by the formation of calcified bars. Some of the cells become eventually enclosed within lacunae, whilst others remain superficial to lay down further bone. As in the case of cartilage-bones, a certain amount of re-modelling occurs, resulting in the formation of Haversian canals and the characteristic disposition of the matrix.

PRACTICAL WORK

Chick embryos may be prepared according to instructions given in text-books of Practical Zoology, and in this connexion the technique described in detail in Marshall and Hurst's 'Practical Zoology' (Eleventh Edition, pages 466–469) is eminently suitable. Prepared slides of chick embryos at successive stages of development should also be studied carefully and drawn. The preparation of embryos of *Oryctolagus* is too technical to be attempted at this stage. It is sufficient to examine and draw prepared slides of embryos of the rabbit at successive stages of development.

CHAPTER 31

Germination

When a seed finds itself in a suitable environment it undergoes a series of changes which may result eventually in its becoming a new plant. The first phases in this series constitute **germination**. Briefly to recapitulate, the mature seed consists of embryo plant, which may or may not lie embedded in a mass of reserve food – the endosperm –, whilst perisperm may be present either in place of, or in addition to, endosperm. The whole is enclosed within a testa, in which a minute pore, termed the micropyle, is perforated. The embryo itself consists of radicle and plumule, together with either one or two cotyledons, in Mono- and Di-cotyledons respectively. In non-endospermic seeds these cotyledons contain the reserve food. At germination fundamental changes occur, resulting primarily in the escape of the whole or part of the embryo plant from the enveloping testa, followed by elongation, growth and differentiation. Germination may be effected in one of two ways, classified according to the behaviour of the cotyledonary portion of the embryo.

Epigeal Germination

The earliest change is the emergence of the radicle through a split in the testa to form the primary root of the plant. In fibrous-rooted plants this is subsequently replaced by lateral branches. The **hypocotyl** is the name applied to the portion of the stem immediately below the cotyledons, and this now elongates rapidly, becoming arched and eventually drawing the cotyledons out of the testa. Immediately above the junction of the cotyledons with the stem is a portion of the stem known as the **epicotyl**, terminating in a bud. In epigeal germination the epicotyl elongates only very slightly at first, so that the plumule lies between the cotyledons, which themselves now commence to effect photosynthesis. This type of germination is described as epigeal, since the cotyledons are carried above the level of the ground. It occurs in both endospermic and non-endospermic seeds, though in the latter the cotyledons are fleshy and contain a supply of reserve food – e.g., the French bean. The castor-oil seed (*Ricinus*) affords an example of epigeal germination in an endospermic seed (see Fig. 327, A).

Hypogeal Germination

As the name suggests this is a type of germination in which the cotyledons are retained below the level of the ground. It is exemplified by the

pea and the broad bean. The hypocotyl does not elongate, but the epicotyledonary bud grows upwards, the cotyledons remaining within the testa. If these are large and fleshy, as in non-endospermic seeds, the

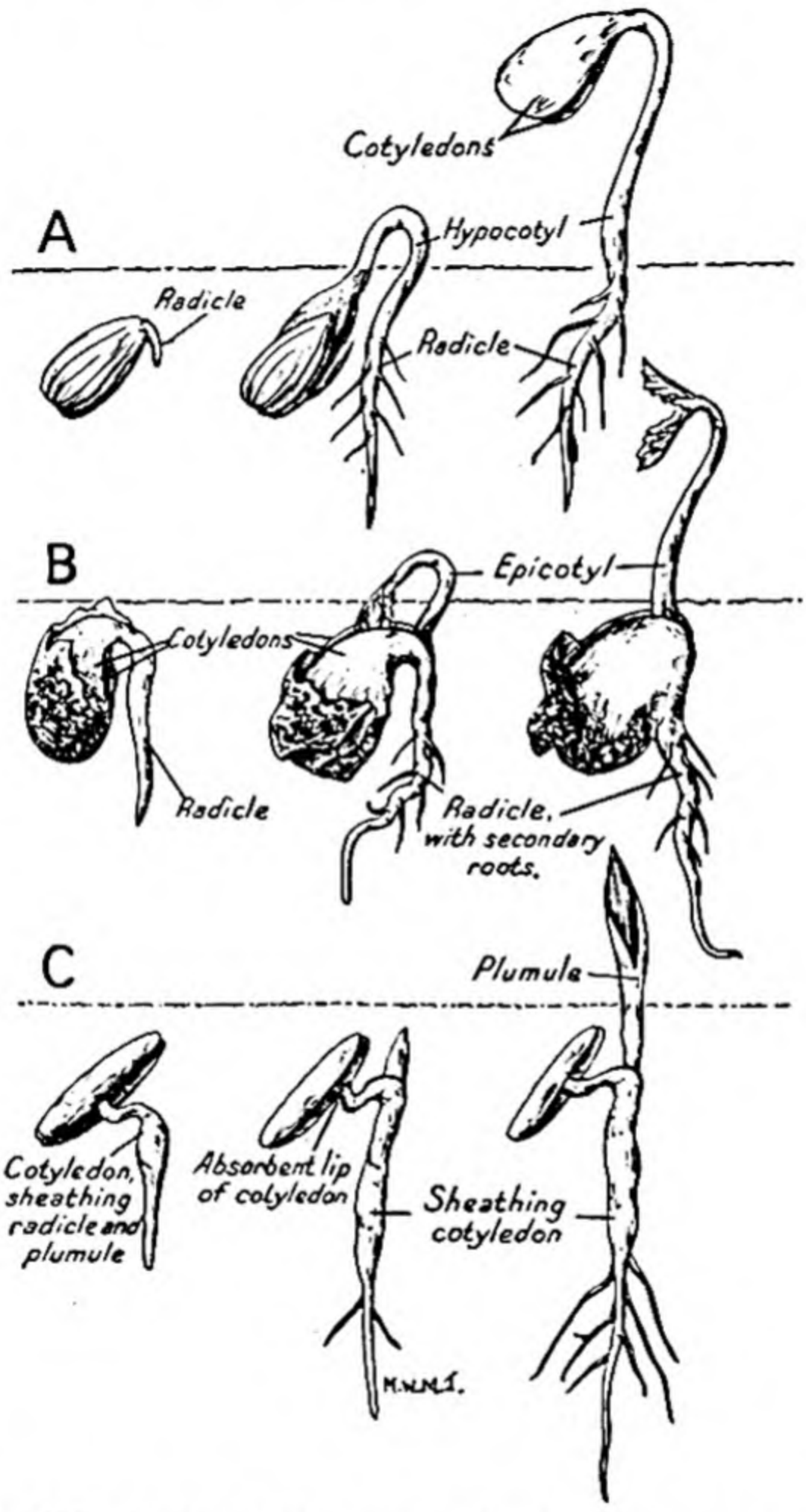


FIG. 327 – Types of germination. For description, see text.

supply of reserve food which they contain is conveyed to the developing seedling via the hypocotyl (Fig. 327, B). In endospermic seeds the surface of the cotyledon in contact with the endosperm produces enzymes which

aid digestion of the latter, after which it is transferred to the seedling. This is well illustrated in monocotyledonous seeds (Fig. 327, C).

Germination of a Monocotyledon

The maize provides suitable material, owing to the size of its grains. A slight oval depression, visible from the outside, marks the position of the embryo, and at one end of this may be discerned the remains of the stigma, indicating that the grain is essentially a single-seeded fruit, the

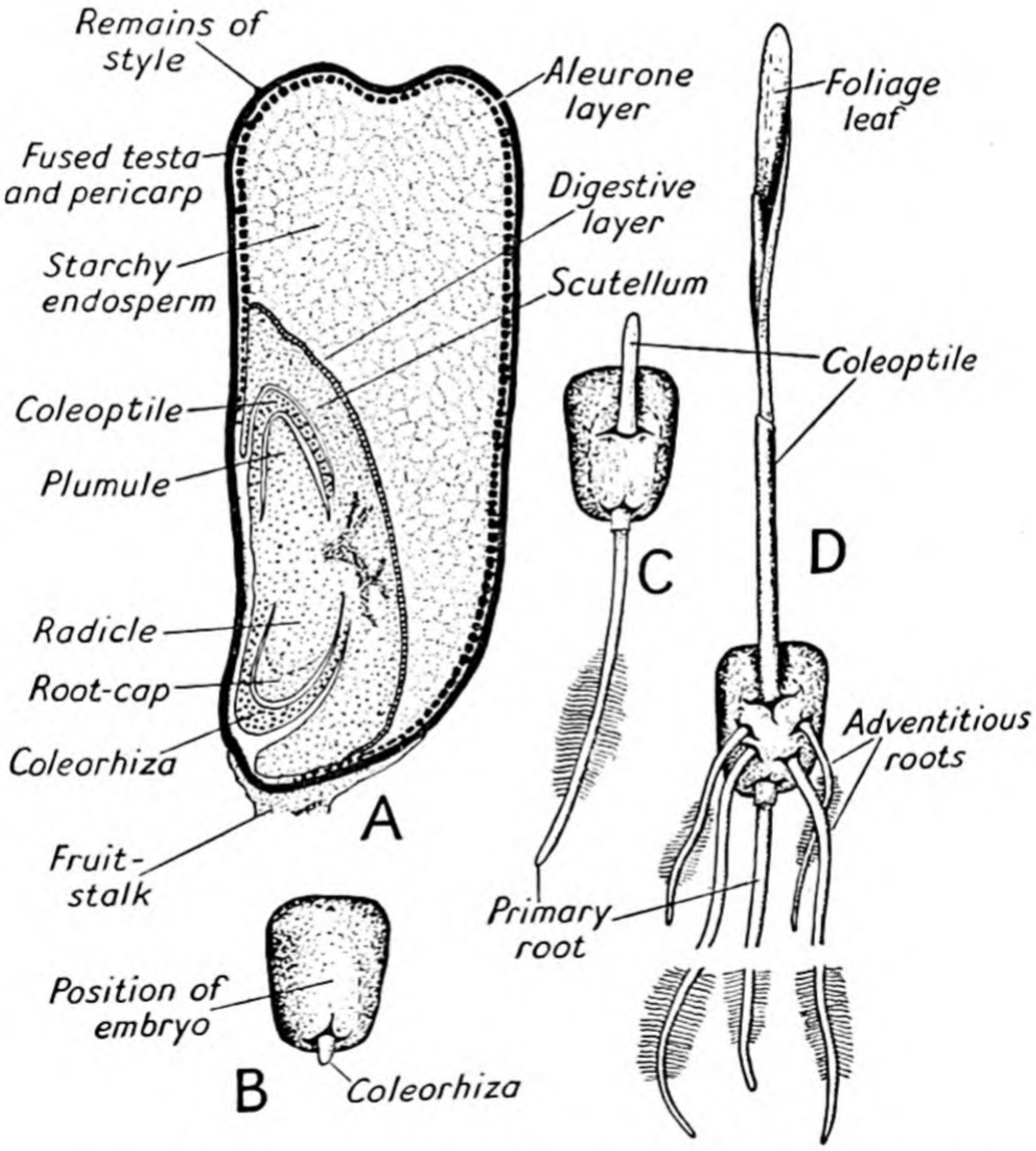


FIG. 328 – Diagrammatic median longitudinal section of the Maize fruit (*A*) and stages in its germination (*B*, *C* and *D*).

testa being fused with the wall of the ovary (pericarp). Within the seed the embryo is distinguishable, embedded in a mass of endosperm. The cotyledon is comparatively large, and encloses the radicle and plumule, pointing in opposite directions. The radicle is enclosed within a root-sheath, whilst the plumule is similarly enveloped by a multi-layered sheath of leaves. On germination the radicle first emerges, forcing its way through its own root-sheath and through the covering of the grain. The radicle does not persist for long, but is soon replaced by adventitious roots from the base of the shoot. After the emergence of the radicle the plumule appears, forcing its way independently through the seed-coat. It grows straight up through the soil, its meristematic tissues being protected by the surrounding sheath, the outermost layer of which is hard and pointed and is known as the **coleoptile**. On reaching the light the inner leaves of the plumule become exposed, each retaining its original sheath around its base. The coleoptile persists as the sheath enclosing the base of the main stem. This type of germination is essentially hypogeal, since the cotyledon remains within the seed, absorbing the endosperm and passing the products to the germinating seedling. It should be noted that some authorities consider the coleptile to be part of the cotyledon.

Conditions of Germination

Reference has been made to the necessity of a suitable environment for germination. Water is one of the principal requirements. This enters the seed, partly through the micropyle and partly through the testa, and without it seeds may remain dormant for very considerable, though varying, periods of time. Wheat grains, for example, may survive up to ten years, whilst acorns perish much more quickly. The germination of 'mummy wheat' is not generally credited. The absorption of water causes the lining of the testa to swell, so that splitting occurs, usually in the region of the radicle, which hence emerges first. Free oxygen is essential for respiration. This would be anticipated in view of the rapid growth which occurs at this time, requiring considerable quantities of energy. It has been shown that a high concentration of carbon dioxide, even in the presence of oxygen, will inhibit germination. This explains why weed seeds, for example, will remain dormant when buried very deep, but germinate when brought up to the surface again. As already seen (page 435), seeds can respire anaerobically for some time after germination has commenced. Finally the temperature must be suitable for germination. Intense cold inactivates protoplasm, whilst too high a temperature quickly results in its coagulation and death. Consequently the temperature must stand at a reasonable mean between these two extremes for successful germination to take place. The effect of light in causing the emergence of the leaves of grasses from the coleoptiles has already been mentioned.

Changes accompanying Germination

The endosperm of a dormant seed consists largely of insoluble material of carbohydrate, protein or fatty nature. In order for this to become assimilable it must first be rendered soluble. This is effected by hydrolysis, assisted by enzymes. Starch is converted to sugar by **diastase**, hemicelluloses to sugar by **cytase**, whilst fats and proteins are acted upon by **lipase** and **protease** respectively. Carbohydrates and fats are of principal significance in the production of energy, whilst proteins contribute to the formation of new protoplasm. Especially is this important at the meristematic tips of the growing seedling, whilst elongation of other parts, notably just behind the tips, is largely a result of the increase in size of the cells due to vacuolation. Their large supply of reserve food material makes seeds an important item of animal diet.

Seeds and Growth Substances

Reference has already been made (page 492 *et seq.*) to substances materially controlling the growth of plant organs. It is desirable now to consider something of the effects which such substances exert on the development of the seedling from the dormant seed. It would appear from experiments on isolated embryos that they are at first lacking in synthetic abilities, owing to shortage of substances of vitamin nature (it is known that vitamins exhibit many hormone characteristics in plants). These substances are normally provided for the embryo from external sources, such as endosperm.

Dormancy in seeds is a phenomenon which has, in the past, been the source of much speculation. It is now suggested as probably due to the accumulation, during early development, of an inhibitor, possibly in the testa, or even in the flesh of fruits. By some means, during the dormant period, this inhibitor is destroyed. In many cases it is possibly leached out of the testa by rain, whilst in others it may be accomplished by the decay of the fruit containing the seed.

It is certain that conditions during the seed's dormant period may affect the subsequent behaviour of the plant resulting from its germination. Thus seeds of winter cereals sown in spring will produce plants which fail to flower unless the seeds are previously retained at a temperature near to freezing point for a minimum period of time. Such treatment is termed *vernalisation*. It is now believed that low temperatures favour the accumulation of a flower-promoting hormone, termed *vernalin*, whilst at higher temperatures this is destroyed.

PRACTICAL WORK

Hypogeal Germination

Examine a pea seed or a broad bean. Note the scar of attachment. Look for the micropyle at one end of the scar. Remove the testa. Note

the two large, fleshy cotyledons. Separate them, and on the inner face of one observe the epicotyl and radicle. Draw.

Line a gas jar with blotting paper and place a few soaked pea or bean seeds between the glass and the paper. Fill the centre space with sand, moistened at intervals. Germination will occur. Sketch various stages.

Epigeal Germination

Repeat the above observations and experiments with castor oil and vegetable marrow seeds. (The food reserve of the former is endosperm and of the latter perisperm.) In the marrow notice the curious heel on the hypocotyl, serving as a mechanism for aiding the extraction of the cotyledons from the testa.

Additional Experiments

(a) Germinate other seeds – e.g., wheat, maize and cress – and decide what is their mode of germination.

In the maize note the absorbent cotyledon, better seen than in wheat, owing to the larger size of the seed.

(b) Immerse seeds in boiling water for a few minutes. Note that they cannot afterwards be germinated, death having resulted from the too high temperature.

(c) Plant seeds in dry sand or sawdust. Notice that no germination occurs. Moisten the sand. Germination takes place, thus proving that water is necessary.

(d) Set up the apparatus shown in Fig. 262 (page 426). Into one limb of the inverted U-tube introduce a few soaked peas, held in position on moist cotton-wool by a tightly-fitting cork. Immerse the open end of the U-tube in alkaline pyrogallol, a powerful absorbent of oxygen. The peas will not germinate. In a control experiment replace the alkaline pyrogallol by water, when germination will occur, thus proving that free oxygen is necessary.

CHAPTER 32

Life-histories of Animals and Plants

Whilst the bodily structure of an animal or plant is adapted to the performance of functions necessary to life, the execution of certain other processes, in many cases not completely necessary to the successful existence of an individual organism, is essential for the perpetuation of the race. Such events constitute the life-history. They are concerned primarily with reproduction, though certain phases, especially in lower animals and plants, accommodate survival in adverse conditions and the distribution of the species to new environments.

Reproduction and Syngamy

Reproduction must result in an increase in numbers, making good the loss to the species occasioned by death. In its simplest form reproduction is effected by fission. This is clearly seen in the Protozoa and some of the lower plants. It involves the sacrificing by the parent of its own individual existence, resulting in the production of two or more daughter-cells. This normally continues as long as conditions remain favourable. But even in these lowly forms the onset of adversity is marked by the production of a resistant body, capable of survival in extremes of temperature and desiccation. Such a body is found particularly commonly amongst the lower plants, where the general term **spore** is applied to it. Its formation is often preceded by the fusion of two cells, a phenomenon known as **syngamy**. Primitively the two fusing cells are identical, nor can they be distinguished from ordinary vegetative cells which, in a favourable environment, undergo fission. The fusion of two such similar cells is termed **isogamy**. In other forms, held to be on a higher plane of evolutionary development, the fusing cells are differentiated. One becomes reduced in size and acquires a considerable degree of motility, whilst the other is passive and laden with reserve food. The fusion of two such cells as these is known as **heterogamy**. It represents the fundamental characteristics of sexual union in all higher animals and plants, where the male element is small and motile, seeking out the female counterpart, in which food is stored for use immediately following the dormant period. But syngamy is obviously not a means of reproduction; it is a mechanism accommodating survival. It results fundamentally in a decrease in numbers, since two cells fuse to form a zygote. Such reduction in numbers

due to syngamy is often secondarily avoided. This may be effected in one of two ways:

(i) By the subsequent fission of the zygote, or

(ii) By the liberation of specialised germ-cells from the parent, so that the individual existence of the latter is not sacrificed.

The former is the method commonly employed by lower animals and plants, whilst in higher forms the latter alternative is invariably adopted. That this is so will be evident from the study of the life-histories of types described in Parts I and II.

Since syngamy so often results ultimately in increase in numbers its performance is often spoken of as **sexual reproduction**. This is perfectly acceptable, providing the fundamental nature of the process is first understood. Reproduction by fission, on the other hand, is distinguished as **asexual**.

In almost all plants and in a few animals both modes of reproduction are practised. At first (in lower Algae and the Protozoa) there is no regular sequence of the two modes, whose occurrence depends on external or internal conditions. Later, however, in all plants from the Bryophyta upwards, sexual and asexual reproduction follow upon each other in a regular cycle. Thus there arises the phenomenon of alternation of generations. This will be considered first in plants, where its occurrence is so universal, and afterwards mention will be made of the existence of a comparable phenomenon in the Coelenterata and Platyhelminthes.

Alternation of Generations in Plants

Of the two generations of all plants above the Thallophyta, one reproduces asexually by means of spores, whilst the other gives rise to gametes, accommodating sexual reproduction. The two generations are therefore known respectively as the **sporophyte** and **gametophyte**. Reference to Chapter 19 makes it clear that sexual reproduction involves an increase in chromosome-number from the haploid to the diploid state. The point in the life-history where the reverse process, the reduction, occurs will be stated individually for each of the groups, now to be considered separately, but in general it can be stated that it is effected in the first division of the spore mother-cell and completed at the second division, since, as already stated, two divisions are necessary for the performance of the entire process.

In the Bryophyta the conspicuous generation, represented by the green thallus, is the gametophyte. This bears antheridia and archegonia, which in turn give rise to gametes. Fusion of these in pairs results in the production of sporogonia. These structures, each consisting of stalk, capsule, and foot, comprise the sporophyte generation. Within the capsule spore mother-cells arise, and each of these divides twice to form four spores. During this process reduction in chromosome-number is effected, so that the spores are haploid. A spore, on germination, gives rise to a new

thallus, all the cells of which contain only the haploid number of chromosomes. The diploid number is restored only at the subsequent fusion of gametes, so that the formation of these latter is not accompanied by a reduction division.

In the Pteridophyta a fundamental reversal of conditions is observed, for here the conspicuous, leafy plant is the sporophyte generation. On the under-surface of the fronds sporangia are borne, and, within the capsule of each, spore mother-cells give rise to spores, a process accompanied by the usual two divisions, in which reduction of chromosome-number is completed. Each spore subsequently germinates to form a prothallus, bearing antheridia and archegonia. This is the gametophyte generation. The spermatozoids and ova, produced within the antheridia and archegonia respectively, fuse in pairs. From each zygote thus formed a new sporophyte arises, remaining for a while attached to and dependant upon the prothallus. As in the Bryophyta there is no reduction division at the formation of gametes. In spite of the obvious dissimilarity between the moss capsule and the fern plant, both sporophytes, they agree in the possession of an epidermis with a cuticle and stomata. This is an interesting feature in view of the subsequent adaptation of the sporophyte to life on land.

In some Pteridophyta, however, the sporophyte generation gives rise to two kinds of spore. An example is provided by *Selaginella*. Both types germinate to form prothalli, but each prothallus bears either antheridia or archegonia, but not both. Such a plant is described as **heterosporous**, foreshadowing the condition in the Spermaphyta.

Alternation of generations is expressed similarly in both the Gymnospermae and the Angiospermae, the fundamental difference between these two groups lying in the condition of the ovule, in the former borne exposed and in the latter contained within the folded carpel. Both groups will therefore be considered as the Spermaphyta. The conspicuous generation is again the sporophyte, giving rise to two kinds of spores – the microspore (pollen grain) and megaspore (embryo sac). Each is developed from a mother-cell, whose division is accompanied by a reduction in chromosome-number. These develop respectively into a male and a female prothallus. The former is represented by the germinated pollen grain and the latter by the mature embryo sac, containing its eight (or seven) nuclei, each surrounded by a layer of cytoplasm. The prothalli bear the gametes – the male cell of the pollen grain and the egg-cell of the embryo sac. These fuse, thus restoring the diploid number of chromosomes in the zygote.

From the above résumé of the conditions of the two generations in the principal divisions of the plant-kingdom a few generalisations may be made. The vegetative cells of the gametophyte generation are haploid in chromosome-number, whilst those of the sporophyte are diploid. The sporophyte is always, at least for a while, parasitic on the gametophyte.

This is obvious in the Bryophyta and Pteridophyta. In the Spermaphyta the zygote (the initial stage of the sporophyte) obtains its nourishment, at least in the early phases of the formation of the embryo, from the contents of the embryo sac, notably the endosperm. In this connexion the position of the seed in this cycle of generations is important. Its various parts do, in fact, represent three generations.

(i) The embryo plant is the young sporophyte.

(ii) The endosperm is the gametophyte (female prothallus?).

(iii) The testa is constituted by the integuments of the ovule, themselves part of the parent sporophyte, whilst any perisperm present is similarly derived, being the remains of the nucellus.

The exact significance of endosperm in Angiospermae is not quite clear. Formed as it is by triple nuclear fusion it is possibly an abortive embryo. Its cells are triploid in chromosome-content, at least to begin with. It will be remembered that in *Pinus* the endosperm arises prior to fertilisation.

Something of the evolutionary significance of the phenomenon of alternation of generations will be considered in Chapter 34.

Alternation of Generations in Animals

It will be remembered that in *Obelia* reproduction occurs either by budding, an asexual method resulting in increase in the number of polyps in a colony, or by the liberation of germ-cells from a medusa. It is apparent that these two modes of reproduction do not succeed each other with the same regularity as do the gametophyte and sporophyte generations in plants, but in principle the phenomena are similar, since even in plants considerable vegetative reproduction frequently occurs. It is so clear in *Obelia* as to require no further elaboration. But in other Coelenterata it assumes a somewhat different appearance. What of *Hydra*, for example? It is obvious that the primary function of the medusa is distribution, and in this it is rendered effective by the fact that it bears the gonads. Does *Hydra* represent forms in which as yet no medusoid stage has been developed, or is it evolutionarily degenerate, having lost its medusa? No definite answer can be given, but an interesting intermediate form may be noticed, namely *Tubularia*. It is a colonial form, the polyps being collected at the head of an attached stalk. It beafs medusae, which, however, are never liberated. This must surely be a degenerate condition, for it is not readily plausible to account for the survival of a form which developed so useless a structure. A medusa more likely appeared as a single step in evolutionary progress. It then became degenerate in some forms, which survived in spite of this loss in powers of distribution. *Hydra* may well occupy a position at the end of this progressive degeneration of the medusoid stage, having regained the power of production of germ-cells. The main point is that the partial development of a medusa, starting from a form in which the medusa was not represented, could be

of no survival value, and hence of no evolutionary significance. Its loss, on the other hand, though perhaps disadvantagous, need not prove fatal to the survival of those forms where this degeneration occurred. In fact the loss of a medusa may even be an advantage. Thus if *Hydra* had one it would inevitably drift towards the sea, in which medium it could not survive. Thus there would be a considerable waste of material.

It should be borne in mind, however, that some authorities see, in the co-existence of medusae on the one hand, and hydranths and blastostyles on the other, in the life-history of *Obelia*, merely an example of polymorphism, with no real occurrence of alternation of generations. This interpretation is supported by the fact that the gametes of the medusae arise actually from cells which had their origin in the ectoderm of the blastostyles. In this case, too, *Tubularia* and *Hydra* may be considered as showing progressive degrees of degeneration.

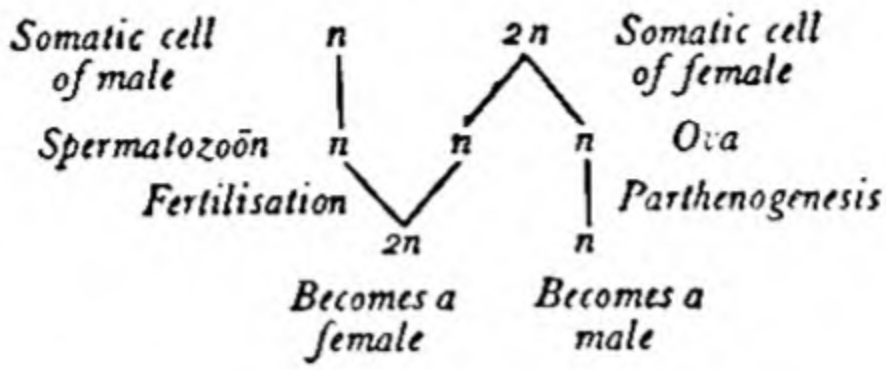
In the class **Anthozoa** of the phylum Coelenterata no medusoid stage is developed, whilst in some members of the class **Scyphozoa** this is the only generation represented. It appears, therefore, to be largely a question of the development of gonads. When one generation comes to develop these regularly, the other is rendered superfluous, and thus disappears from the life-history.

In the Platyhelminthes alternation of sexual and asexual modes of reproduction is commonly encountered. Thus in the liver fluke (page 42) considerable multiplication by asexual means occurs between the liberation of a fertilised egg and the formation from it of a new generation of adults. In *Taenia*, too, strobilisation (page 48) may aptly be regarded as a mechanism of asexual reproduction, facilitating as it does the dissemination of so great numbers of eggs. Certainly *Taenia echinococcus* displays asexual reproduction in that it multiplies in the cysticercoid stage.

Parthenogenesis

Occasional reference has already been made to the development of eggs without previous fertilisation. It is represented commonly amongst the Insecta, whilst an example is afforded by *Alchemilla* (lady's mantle) amongst plants, producing seed without fertilisation. It is obvious that some modification of the normal behaviour of chromosomes must occur, since there is no fusion of nuclei to restore the diploid number. In the honey bee, for example, eggs and spermatozoa, like all gametes, contain the haploid number of chromosomes. The fusion of sperm with an egg nucleus restores the diploid constitution, and such a fertilised egg becomes a female. An unfertilised egg, however, may develop into a male, whose somatic (body) cells will therefore contain only the haploid number of chromosomes. Thus, when a female gives rise to eggs there must be a reduction in chromosome-number, but in the production of spermatozoa no such reduction occurs, since the cells from which they are formed also

contain only the haploid number of chromosomes. This condition of the chromosomes may best be made clear by the following figure:



In other cases the number of chromosomes in the egg developing parthenogenetically is maintained diploid by the fusion with the egg of one of the polar bodies (page 320). See also page 583.

Apogamy in plants is the phenomenon involving the vegetative origin of the sporophyte from the prothallus, sexual organs playing no part. It is exemplified commonly by ferns. This is closely akin to the production of seed without fertilisation, as already mentioned above.

A peculiar instance of parthenogenesis, to which the term **paedogenesis** is applied, is encountered exceptionally amongst animals. It differs from ordinary parthenogenesis in that the eggs are produced by immature females. An example is afforded by the axolotl, an Amphibian which never passes beyond the larval stage of a species of salamander. This animal is further interesting in that, like other salamanders, it is viviparous. It can usually be made to undergo metamorphosis by the subcutaneous (i.e. beneath the skin) implantation of crystals of iodine, whilst the same process may occasionally be effected if the water level is lowered and the animal forced to breathe air. In both cases, as in that of all the Amphibia, the metamorphosis is chiefly due to the modification of the activity of the pituitary and thyroid glands.

Sex and Reproduction in Animals

In all forms above the Coelenterata sexual reproduction is the only mode regularly practised by animals. There is clear differentiation of gametes into male and female, whilst certain features become characteristic of the animals producing them. In most cases the sexes are separate, so that the organisms themselves, as well as the gametes, are distinguishable as male and female. In a few instances the same animal produces both eggs and spermatozoa, being then described as **hermaphrodite**. It is important to notice that even in hermaphrodite forms cross-fertilisation is the general rule, except where special conditions – e.g. parasitism – prevent it.

Fertilisation

The essential feature of sexual union is the fusion of a spermatozoön with an egg. This constitutes true fertilisation of the egg. The term has become extended, however, to include the mechanism whereby the eggs and sperm are brought into contact. The gradual perfecting of this process in the various classes of vertebrates is interesting and instructive. In fish there is customarily a return in shoals to a breeding ground, where, without recourse to pairing, eggs and spermatozoa are deposited. It is purely fortuitous whether or not the eggs are fertilised, and this involves a very great wastage of material. A single female cod, for example, lays some three million eggs in a breeding season. Fertilisation is here described as external. In a few exceptional forms – e.g. *Scyliorhinus* – it is internal (page 108).

In most Amphibia, exemplified by the frog, fertilisation is still external, but pairing occurs, as described on page 136. In this way the chances of an egg becoming fertilised are very considerably enhanced. Development of the eggs is still entirely dependent upon external conditions.

In birds fertilisation is internal. The male introduces spermatozoa into the base of the genital tract of the female, whilst the eggs are fertilised in the oviduct. Following fertilisation a shell is secreted about each egg, which is subsequently shed to the exterior. In many cases incubation is effected by heat from the body of the mother.

In Mammalia both fertilisation and development are internal. Eggs are produced in a pair of ovaries, whose characteristic structure in this class was described on page 346.

Sperms are introduced by the male into the vestibule of the female by the penis, erection of which is effected by an increase in blood-pressure. On reaching the oviduct, largely as a result of muscular contraction in the female tract, a sperm must penetrate three covering layers of the egg proper. The first of these consists of several rows of follicle cells. Sperms penetrate the matrix between the follicle cells, causing their partial dispersal, with the assistance of an acrosomal enzyme. Thus a greater target area for the sperms is presented, whilst the inter-cellular channels created direct the sperms towards the egg. Within the follicle cells is the mucoproteinous *zona pellucida*, to which sperms become attached by the acrosome, presumably as a result of some specific adhesion (page 516). The penetration of the zona can occur only after sperms have been for some time in the female tract, where a phenomenon, termed *capacitation*, occurs, resulting in the liberation of the necessary enzyme from the acrosome. Finally the successful sperm becomes attached to the vitelline membrane before the whole of it is engulfed by egg cytoplasm. The ultimate entry stimulates the egg to development and so changes the enveloping layers that further penetration by sperms is impossible. The nuclear membranes of both egg and sperm disintegrate, and the now double group of chromosomes proceeds to mitosis. It is quite possible

that parts of the sperm other than the nucleus may influence the initial stages of development. Soon the developing embryo passes down into the uterus, where it presently forms a **placenta**, a thickening in the wall of the uterus to which it is vitally attached by a stalk, or **umbilicus**. Along this the developing embryo, known in this condition as a foetus, receives nourishment and oxygen, whilst its waste products are similarly removed. When the period of gestation – retention within the uterus – is complete the foetus is completely developed, as a miniature edition of the adult. By the contraction of the walls of the uterus and abdomen it is forced to the exterior, after which the remains of the placenta and embryonic membranes are shed as the 'after-birth'. The young are subsequently nourished on a milky fluid produced in the mammary glands of the mother.

Thus there is a gradual perfecting of the process of fertilisation, accompanied by a progressive reduction in wastage of material and increase in the chances of successful development of the embryo after fertilisation.

Life-histories of Animals and Plants Compared

In the Protozoa and some Thallophyta reproduction is effected by simple or multiple fission as long as conditions remain favourable. Syngamy occurs in times of adversity. In plants – e.g. *Spirogyra* – this results in the formation of a resistant zygospore. In animals a resting stage is less universal. In *Paramecium*, for example, conjugation results in rejuvenescence, the meganucleus being replaced as a result of division of the product of fusion of the products of division of the micronuclei of both conjugants. The zygotic nucleus, formed by the fusion of two nuclei, will possess a new gene-complex (see page 576), thus maintaining variability for the operation of natural selection. The formation of a resting stage in the life-history of plants does, however, find a parallel in that of those animals which cannot restrict reproduction to favourable seasons, or else deliberately use the egg as a means of overcoming periods of adversity. This is clearly exemplified by most insects in temperate climates. The fertilised egg of most higher animals, however, must soon develop or perish. A seed is produced as a result of fertilisation. But a hen produces an egg whether fertilisation has or has not taken place. There is no apparent difference between the fertilised and unfertilised egg, but it is obviously the former alone which will, on incubation, give rise to a chick. A seed, on the other hand, is not formed, except on rare occasions, without previous fertilisation of the egg-cell of the embryo sac. This fertilisation results in severe changes in the ovule itself, possibly including the formation of endosperm and the modification of the integuments to form the testa. Both eggs and seeds normally contain a supply of reserve food material for the development of the embryo, though in mammals this has been reduced almost to vanishing point, in accordance with the retention of the foetus within the uterus. It must

be very clearly realised that the above comparison is one of function only. No comparison of individual structures in egg and seed can be made in any sense. At the very most an egg and seed may be regarded as analogous (page 595). Enough has been said already concerning the regular alternation of sexual and asexual modes of reproduction in plants, a phenomenon but poorly represented in animals. In both animals and plants the number of eggs or seeds produced is inversely proportional to their chances of survival. Those containing but little food are normally liberated in large numbers, since there is nothing on which the embryo or seedling can live, and therefore survival depends on the almost immediate finding of a suitable environment, which may occur in only a small percentage of cases. Eggs with much yolk, embryos retained in the body of the mother, or seeds with copious reserves of food are less dependent on external conditions. Thus they are produced in much smaller numbers.

Specialised Life-histories

Reference must be made in conclusion to a few instances where the life-history has become secondarily modified. So far in the present chapter only those types of animal development have been considered in which the fertilised egg develops more or less directly into a miniature adult. But in others there is formed an intermediate stage, leading a free and independent existence, yet markedly dissimilar from the adult. The two best examples of this phenomenon are afforded by insects and Amphibia. The egg of some insects – e.g. a moth – develops first of all into a caterpillar, unlike the adult (imago), yet leading an independent existence for some time. Such a stage is known as a **larva**. Eventually this becomes enclosed within a cocoon, forming the **pupa**. Within this case a rapid series of structural changes occurs, resulting in the assumption of adult form. This series of changes constitutes **metamorphosis**. The full life-history may therefore be summarised as follows:

Imago → fertilised egg → larva → pupa → imago.

Development of the frog has already been described (Chapter 29) and there the same phenomenon of indirect development via a larval stage will have been observed. In both instances the larva fulfils a special purpose in the life-history. In the butterfly the caterpillar is a voracious feeder and grows rapidly. The pupa is adapted for the conversion of what is virtually one animal into another, whilst the imago distributes the species, reproducing and laying eggs on an abundant food-supply. The larval tadpole of the frog is an adaptation to development in water of a form which subsequently becomes partly terrestrial.

The life-histories of parasitic animals and plants have already been described in some detail (Chapter 1, 3 and 11). In every case they are complicated, increasing the probability of the infection of new hosts. In

plants, where this is relatively easy, rapid production of spore-like bodies occurs as long as conditions remain favourable, whilst in adversity resistant structures are formed. In animals the problem of infection is more severe, so that the life-history becomes variously modified, as already described for certain parasitic Protozoa and Platyhelminthes.

PART VI

Heredity and Evolution

In previous chapters the various visible stages in development of animals and plants have been described. It remains now to gain some idea of the problem of inheritance of parental characters by the offspring. It is evident on reflexion that not only are the broader features of structure handed on from one generation to another, but detailed resemblances are apparent between parent and offspring, as may be discovered by a study of the members of many human families. The mechanism by which such inheritance is effected will be considered, together with a brief description of some of the more important experimental work on which present-day conclusions are based. It must be borne in mind that only the barest outline of a few facts selected from a wealth of material can be given, and that mainly in the hope of stimulating the student to a further pursuit of the subject of genetics.

Whilst heredity is concerned with the explanation of similarity between parent and offspring, and thus with the stability of structural form, evolution postulates a continuous changeability. Evidence for this will be briefly considered, and in conclusion the more important theories to account for it will be outlined. Especially in connexion with the evidence for evolution should the student be able to make use of knowledge already gained to build up a case in its favour. Here chief emphasis will be laid on points not previously described or discussed.

CHAPTER 33

The Mechanism of Inheritance

Resemblances, including those of a detailed nature, between parents and offspring are due to heredity. Differences between parents and offspring are due to variation, which may itself be of hereditary nature or determined by environment. **Genetics** is that branch of biology dealing with heredity and variation. The study of inheritance is inseparable from the name of the abbé Mendel. Gregor Johann Mendel, an Austrian by birth, entered the Augustinian monastery at Brünn in 1843, becoming abbé in 1860. In the cloister gardens of his monastery he carried out his immortal researches into the laws of inheritance, employing for this purpose the garden pea, *Pisum sativum*. His results, published in 1866, remained neglected until 1900, when their importance was realised simultaneously by several distinguished biologists. Although by no means the first in the field to investigate hybridisation in plants, Mendel simplified the problem by concentrating upon either one or two selected characters and his methods are worthy of careful study. Flowers of the garden pea are often self-pollinated. In order to avoid this, Mendel removed the stamens from some of his selected flowers and subsequently placed upon the stigmas of these de-stamenised flowers pollen from plants which he required to use as the other parents in his experimental crosses. Every possible precaution was taken to prevent pollination by any other means – e.g. access to these flowers by insects had to be denied. In this way Mendel was able, under fully controlled conditions, to cross two plants differing in respect of one specific characteristic, such as flower colour or plant height. Having examined the hybrid plants in respect of the character concerned, he then allowed them to inter-breed and thus obtained a second generation, no de-stamenisation this time being necessary. Thus, for example, Mendel crossed coloured-flowered plants with those with white flowers and found that, in the hybrids, all the flowers were coloured. Inter-breeding of these hybrids resulted in the production of plants with coloured flowers and those with white in the ratio of 3 to 1. In order to obtain this ratio Mendel dealt in relatively large numbers. Thus in one experiment of the type quoted above he obtained 705 plants with coloured flowers and 224 plants with white flowers. Reference to this point is made again below.

Mendel then extended his investigations to the simultaneous examination of two characteristics of his experimental plants – e.g. seed coat form (smooth or wrinkled) and the colour of the seed coat (green or

yellow). But his method remained the same – perfect control of breeding possibilities by the previous removal of the stamens from those flowers destined to give him his hybrid seeds.

As a result of his investigations Mendel postulated the existence of something transmitted from parent to progeny in the gametes and being responsible for the determination of such contrasting characters as coloured and white flowers. This 'something' is what we now term a gene. It is with the nature and behaviour of genes that genetics is concerned. Without knowledge of the existence of such particles, Mendel formulated two generalisations, popularly termed his 'Laws of Inheritance'. They are:

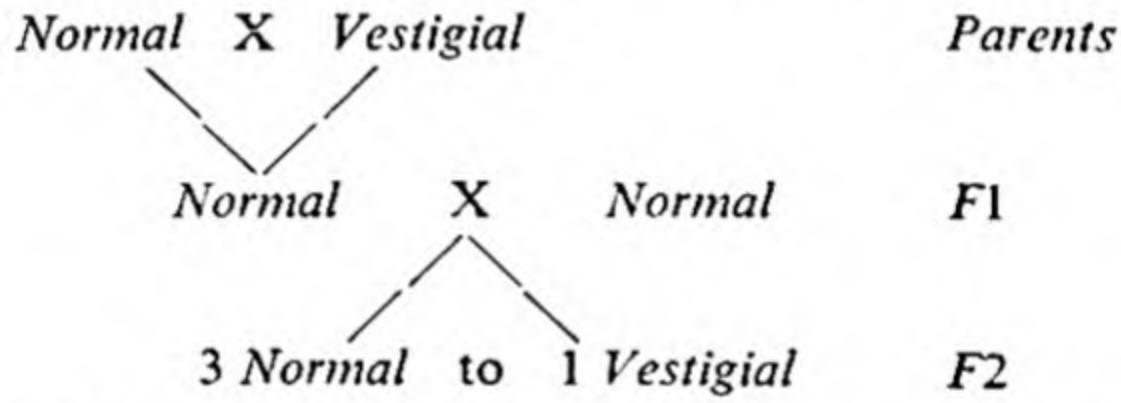
I. THE LAW OF SEGREGATION. This implied that, in the hybrid state, different genes do not blend or in any way contaminate each other, whilst they eventually segregate to pass into different gametes and hence to different members of the second generation produced by interbreeding of the hybrids.

II. THE LAW OF INDEPENDENT ASSORTMENT. From such crosses as Mendel performed involving two characters simultaneously, he came to the conclusion that the segregation of the members of any one pair of contrasted genes (e.g. those for green or yellow seeds) in no way influenced the behaviour of the members of any other pair (e.g. those for smooth or wrinkled coat). In other words, gametes from such a hybrid plant could contain any one of the four possible combinations of genes – yellow/smooth, yellow/wrinkled, green/smooth, green/wrinkled. This again is a pointer to the necessity for using large numbers, thereby affording opportunity for all these combinations to occur reasonably equally. As will be seen later, this law is not universally applicable. Most of the examples quoted in the following pages will be drawn from animal sources, but it must be remembered that the same mechanism is responsible for the transmission of hereditary traits in plants, to which occasional reference will be made.

Monohybrid Ratio

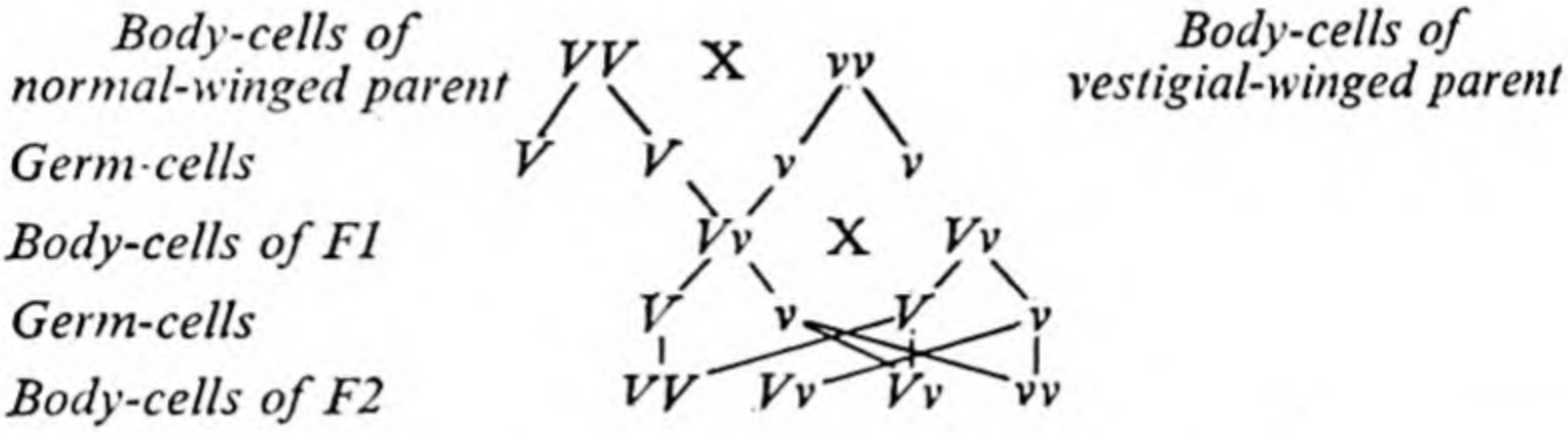
One of the most extensively investigated animals is the fruit-fly, *Drosophila melanogaster*. It is ideally suitable for such experimentation, for it has a considerable number of easily recognisable, sharply contrasted characteristics, it breeds prolifically in captivity and is reasonably hardy. The first character for consideration is that of length of wing. This manifests itself in two forms – normal and vestigial. The first requirement in any such genetical experiment as that described below is to obtain pure lines from which the parents may be selected. This is done by continued breeding through many generations and the weeding out of all those progeny which do not show the given character in the desired form. Thus, starting with two normal-winged insects, this procedure is adopted until such times as no vestigial-winged forms ever make their

appearance. It can then safely be assumed that a pure normal-winged strain has been obtained. To obtain a pure line of vestigials one such fly is mated with a normal. The offspring of this cross are then inter-bred and vestigials selected for further inter-breeding. In three generations a pure line of vestigials is thus obtained. Two parents are then selected from these strains and mated. It is found that all the offspring so obtained are normal winged – just the same as the original normal parents, though it is obvious from their origin that these offspring are hybrid. Breeding between these normal-winged progeny of the first generation (known as the first filial generation and therefore styled the *F*1) results, in the second generation (the *F*2), in the production of normal- and vestigial-winged forms in the ratio of 3 to 1. This is known as the **monohybrid ratio** and may be defined as the ratio obtained in the second generation from original pure parents differing in respect of one character. (It must be noted that only *one* character – wing-length – is involved: 'normal' and 'vestigial' are different manifestations of that character.) The results of the crosses indicated above may be summarised thus –



EXPLANATION. In the normal-winged parent every cell of the body (as distinct from germ-cells) contains two **genes** for normal wing. The nature and mode of operation of genes are more fully discussed on page 575, but for the moment it will suffice to think of them as highly specific, molecular aggregates, borne in linear array upon the chromosomes. Those for any given character are borne in a fixed position (*locus*) on both members of a particular pair of homologous chromosomes (page 313). In the vestigial-winged parent the same chromosomes bear, at the same locus, genes for vestigial wing. Now prior to germ-cell formation meiosis (page 316) occurs. Thus every germ-cell, whether egg or sperm, can contain only one member of the given pair of chromosomes, and hence only one gene for wing-length. At fertilisation the pair of chromosomes is restored, but it follows that every cell of the body of any member of the *F*1 generation will contain one gene for normal wing and one for vestigial wing. Since the gene for normal wing over-rides that for vestigial wing (the *F*1 are all normal winged) it is described as *dominant*, whilst the gene whose influence is suppressed is described as *recessive*. This is discussed more fully on page 578. When the progeny themselves produce germ-cells they will obviously form in equal numbers those with a gene for normal wing and those with a gene for vestigial wing. When they

interbreed in large numbers the sperm/egg combination in respect of these genes is purely a matter of chance – e.g. it is just as likely for a sperm containing a gene for normal wing to fertilise an egg containing a gene for normal wing as it is for it to fertilise an egg containing a gene for vestigial wing. These results, in terms of genes, may be expressed as shown below. It is a commonly accepted convention that the recessive gene is represented by the small form of the initial letter of the character produced – i.e. v = vestigial. The corresponding dominant gene is represented by the capital form of the *same* letter – i.e. V = normal-winged. This notation serves to emphasise that both genes are for the same character, whilst one (V) is dominant to the other (v).



All members of the $F2$ generation containing the gene V will be normal winged, whilst only vv can be vestigial winged. Thus the ratio of 3 to 1 is accounted for, though again it must be emphasised that, in order to obtain it, it is essential to deal in large numbers.

Vocabulary

The above example may be used to illustrate the definitions of some of the basic terms fo the geneticist's vocabulary.

ALLELOMORPHS. These are the genes for any given character, borne at the same specific locus on both members of a given pair of homologous chromosomes in every body-cell (see also page 581).

Thus the genes for wing-length, whether V or v, are allelomorphs.

HOMOZYGOUS. This is the description given to the condition where the two allelomorphs for the character under consideration are identical.

This is so, for example, in the original 'pure' parents, which were respectively VV and vv. A *homozygote* is thus an organism in which this condition is fulfilled.

HETEROZYGOUS. This is the description given to the condition where the two allelomorphs for the character under consideration are contrasting.

This, in fact, amounts to the hybrid condition, where the genes V and v are present together. An organism in this condition is termed a *heterozygote.*

DOMINANT. A gene is said to be dominant if it expresses itself fully

even when present in the heterozygous condition.

RECESSIVE. A gene is said to be recessive if it is totally suppressed when present in the heterozygous condition.

Thus the gene *V* for normal wings is dominant over *v*, responsible for vestigial wings and itself recessive.

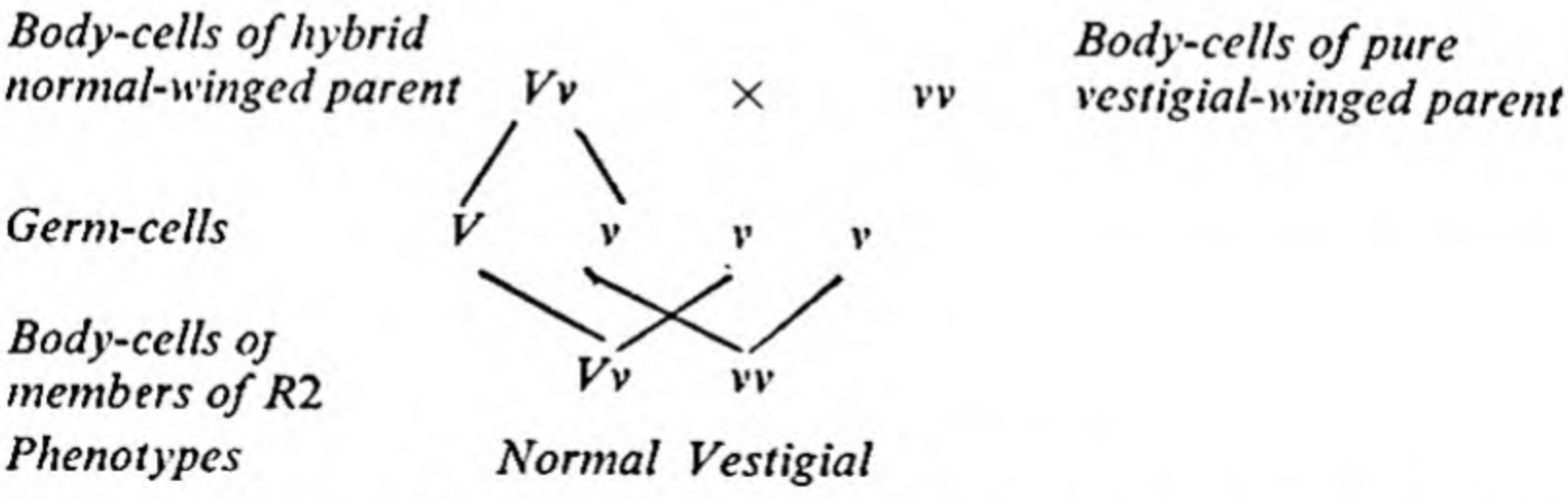
The problem of dominance is often more involved than is suggested here, but it is best first to establish the basic principles of genetics before discussing refinements. Accordingly this subject is referred to again on page 578.

PHENOTYPE. The phenotype of an organism is the quality apparent upon inspection in respect of the character under consideration.

Thus pure normal-winged and hybrid normal-winged flies have the same phenotype – i.e. they appear as normal-winged.

GENOTYPE. The genotype of an organism is its actual genetic constitution in respect of the character under consideration.

Thus, in the example quoted above, although pure and hybrid normal-winged flies are of the same phenotype, they are of different genotypes, the former being *VV* and the latter *Vv*. But since the gene *V* is dominant it expresses itself fully in the hybrid condition. Manifestly the only method of determining the genotypes of similar phenotypes is to use them in breeding tests. This is done by what is termed a **back-cross**. In this, unknown genotypes are mated with a parent with the phenotype of the recessive gene (i.e. one in which the recessive gene is present in the homozygous condition). Thus if a *pure* normal-winged form is mated with a pure vestigial-winged parent *all* the offspring will be phenotypically normal in wing-length. This cross is shown on page 570. But if a *hybrid* normal-winged fly be bred with a recessive vestigial-winged insect, normal-winged and vestigial-winged offspring will be produced in equal numbers. Such a generation is styled the *R*2, distinguishing it from the *F*2, where hybrids are inter-bred. Thus –



Again, the numbers involved in these crosses must be large so as to ensure equal opportunities for the germ-cells (all *v*) of the vestigial-winged parent to combine with either type of germ-cell (*V* or *v*) of the hybrid normal-winged parent.

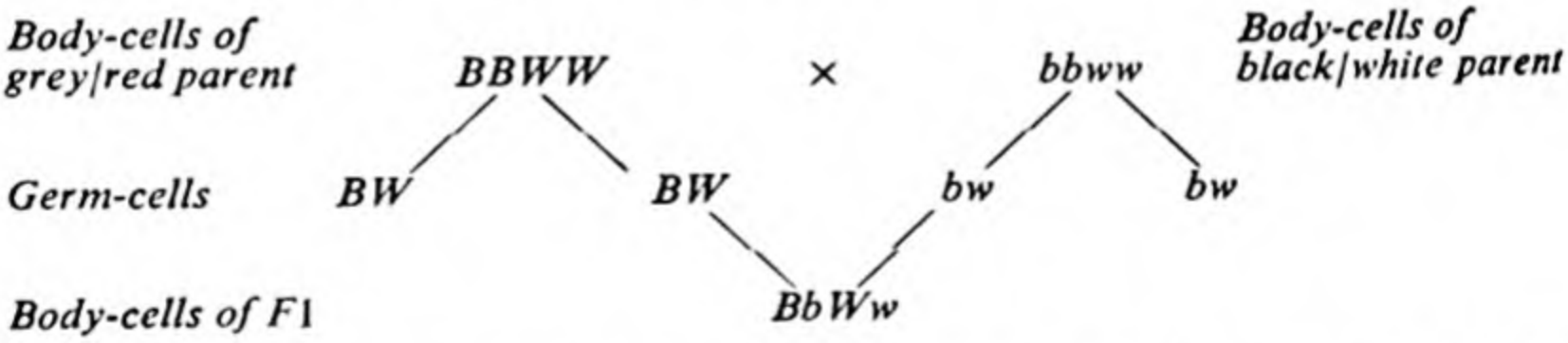
Dihybrid Ratio

This is comparable with the monohybrid ratio discussed above, but here the simultaneous inheritance of two characters is investigated. It may be defined, in fact, as the ratio obtained in the second generation from original parents differing in respect of two characters. Taking an example again from *Drosophila*, the original parents are grey-bodied and red-eyed, and black-bodied and white-eyed respectively. Since all members of the *F*1 generation are grey-bodied and red-eyed, it follows that the genes for these characters are dominant. When members of this *F*1 generation are inter-bred, the progeny (*F*2) are grey-red, grey-white, black-red and black-white in the ratio of 9:3:3:1. This is the **dihybrid ratio**.

EXPLANATION. Based on the conventional system, the genes will be represented –

b = black-bodied;	B = grey-bodied
w = white-eyed;	W = red-eyed

Thus every body cell of the original parents, which must be homozygous if a true ratio is to be obtained in the second generation, will contain (*a*) two genes for grey body and two genes for red eye, and (*b*) two genes for black body and two genes for white eye. It follows that the germ cells to which they give rise will contain one gene only for each character. Thus the first cross may be tabulated –



In the formation of germ-cells by members of the *F*1 generation a very important principle is involved. It must be assumed that the genes for body-colour and eye-colour are borne on *different chromosomes* and hence that they can separate independently. (What occurs when genes for characters under consideration are on the *same chromosome* will be considered later in the present chapter.) Thus, when germ-cells are being formed by members of the *F*1 generation, the chromosomes concerned may segregate at meiosis (page 316) in two possible ways, namely, the one bearing the gene for grey body may accompany that bearing the gene for red eye (in which case simultaneously the chromosomes bearing genes for black body and white eye respectively will associate), or, alternatively, the chromosome bearing the gene for grey body may accompany that bearing the gene for white eye (with the corresponding association of the chromosomes bearing the genes for black body and

red eye). In other words, as indicated in the diagram below, there are four possible types of germ-cell. Again it becomes evident that the numbers of insects used in such a cross must be sufficiently high as to make it mathematically probable that all will be produced in equal numbers. With four types of germ-cell being produced by every parent, it follows that there are sixteen possible combinations – another excellent reason for dealing in large numbers, thereby ensuring reasonably equal opportunity for all of them to occur. The possible results anticipated in the *F*2 generation may therefore be represented as follows –

	BW	*Bw*	*bW*	*bw*
BW	1 *BB* *WW*	2 *BB* *Ww*	3 *Bb* *WW*	4 *Bb* *Ww*
Bw	5 *BB* *Ww*	6 *BB* *ww*	7 *Bb* *Ww*	8 *Bb* *ww*
bW	9 *Bb* *WW*	10 *Bb* *Ww*	11 *bb* *WW*	12 *bb* *Ww*
bw	13 *Bb* *Ww*	14 *Bb* *ww*	15 *bb* *Ww*	16 *bb* *ww*

Thus genotypes in squares 1, 2, 3, 4, 5, 7, 9, 10 and 13 (i.e. 9 in all) will yield phenotypes which are grey-bodied and red-eyed, since at least one dominant gene is present for each of these characters. The genotypes in squares 6, 8 and 14 will develop into grey-bodied and white-eyed phenotypes, whilst squares 11, 12 and 15 represent black-bodied and red-eyed phenotypes. Only in square 16 are both recessive genes present in the homozygous condition and hence only this genotype can produce black-bodied and white-eyed offspring. Thus the dihybrid ratio of 9:3:3:1 is accounted for.

Linkage

In the investigation of the dihybrid ratio it was specifically stated that the genes for the characters under consideration were necessarily borne on different chromosomes. Where two genes are carried on the *same* chromosome they are said to be linked. In normal circumstances (see

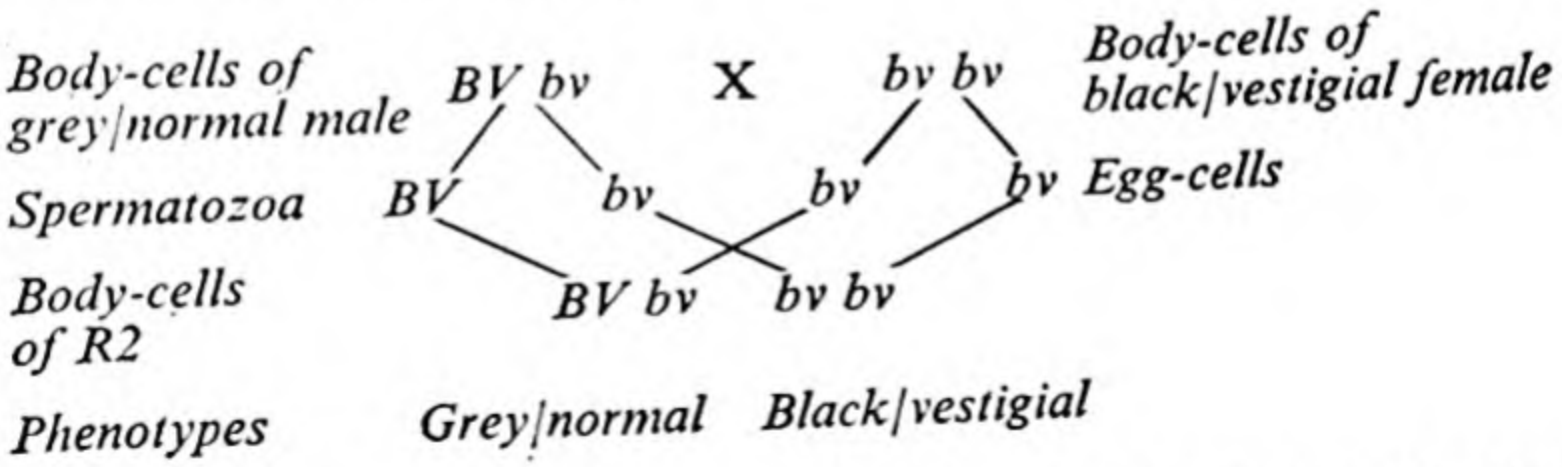
below) they will therefore be inherited together, for, being on the same chromosome, they are inseparable. Thus, in *Drosophila*, if a member of a pure line with grey bodies and normal wings is mated with a member of a pure line with black bodies and vestigial wings, all the offspring will be grey-bodied and normal-winged. This gives no clue to the disposition of the genes. But if members of the *F*1 are inter-bred, the *monohybrid* ratio of 3 grey-normal to 1 black-vestigial, and *not* the dihybrid ratio, is obtained. Thus the genes for these characters are linked. It has been shown in *Drosophila* that there are four groups of characters normally inherited together. At the same time, *Drosophila* has four pairs of chromosomes, each obviously carrying the genes for one of these groups.

Crossing-over

But such simplicity of results is varied by the occasional appearance of progeny in which the characters normally inherited together become separated, resulting in the production of aberrant grey-vestigial and black-normal forms. This has been most helpfully investigated by the technique of back-crossing (page 573) hybrid grey-bodied, normal-winged forms with homozygous recessive parents (black-bodied and vestigial-winged). It is found that if *male* hybrids are mated with black-vestigial females all the offspring are grey-normal and black-vestigial in equal numbers, with no aberrant forms. This is what would be anticipated, such a mating being tabulated thus –

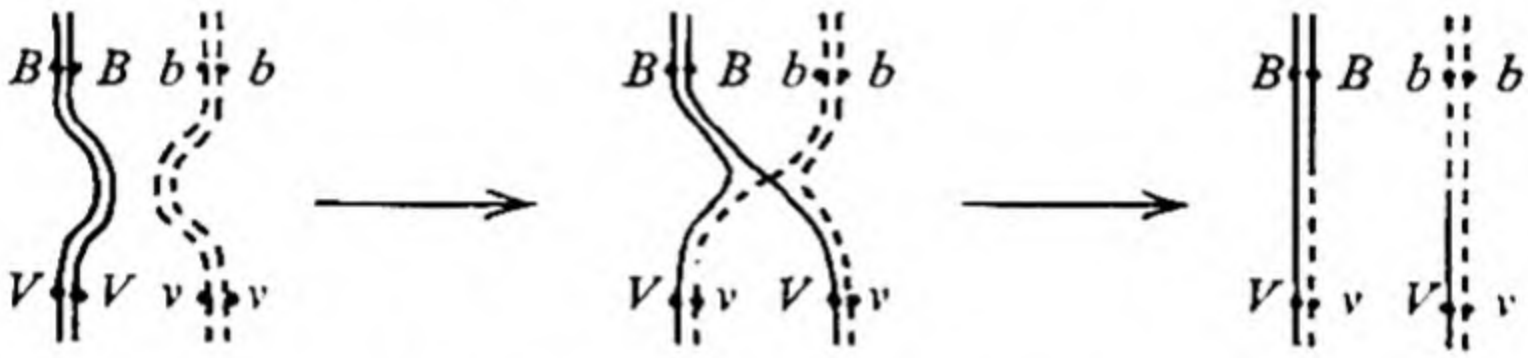
Let b = black-body; B = grey-body
v = vestigial-wing; V = normal-wing

It should be noted that the genotypes are written *BVbv*, for example, and *not BbVv*. This is done wherever linkage is involved. To write the genotype *BbVv* implies that the genes for the characters concerned are on different chromosome pairs.

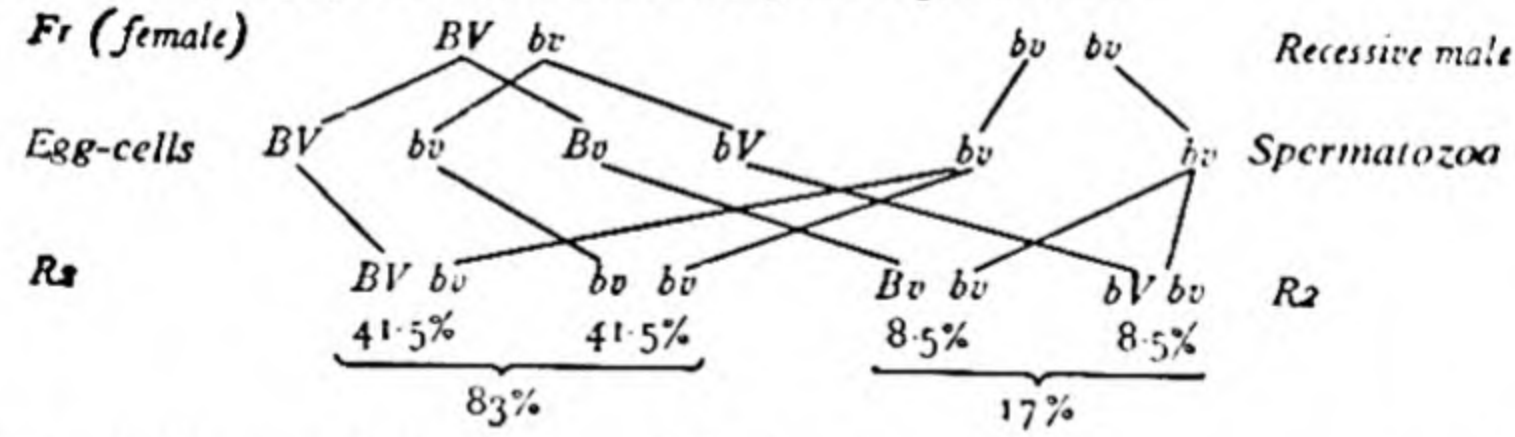


But if the sexes are reversed and *female* hybrids are mated with recessive males, then only 83% of the offspring are of phenotype grey-long and black-vestigial (41.5% of each), whilst the remaining 17% are equally grey-vestigial and black-long. In order to achieve these results the genes for the characters exhibited by the female must have been separated in 17% of the egg-cells formed, instead of the chromosomes' continuing

as expected – as unbroken units. This can be accounted for as a result of certain chromosomal behaviour witnessed during meiosis. At the stage concerned the chromosomes are already divided longitudinally into chromatids (page 313). As a result of spiralisation of the chromonemata (page 313) and the relational coiling of homologous pairs of chromosomes, tensions are set up, causing breaks at weak points in one of the chromatids of each pair. As these broken ends fly outwards, they meet and join up with the broken ends of the other snapped chromatid. Chiasmata appear as a result of these fractures and reunions and thus represent the junctions between chromatids of maternal and paternal origin respectively. Since only one member of each pair of chromatids is involved, the cross-over value for any given pair of genes can never exceed 50%. In the case under consideration it is clear that fracture and reunion of the portion of the chromatids between the genes for body-colour and wing-length occurs in only 17% of completed meioses. Such crossing-over may be represented diagrammatically as follows



The results, then, of such a cross may be represented –



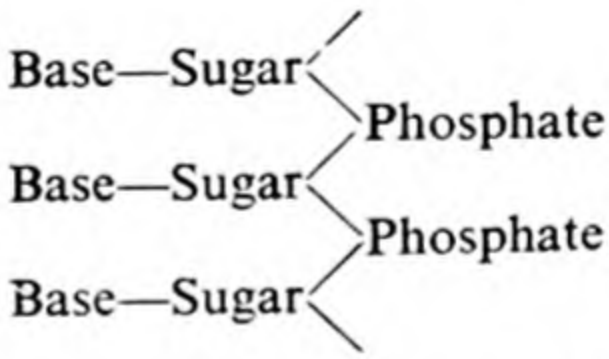
It should be noted that *Drosophila* is unique in that crossing-over does not occur in the male.

Composition of Chromosomes

It is abundantly clear from a study of the foregoing pages that the gene is a unit of function. This led to the concept of a chromosome being comparable with a string of beads, each of which represented a gene. But the fact that crossing-over has been shown to occur between what were formerly regarded as allelomorphs makes such a view untenable. More likely is it that genetic material is structurally continuous throughout the chromosome and that the genes merely represent segments of it.

As has already been indicated (page 394) the specific nature of the

tissues of any organism is largely resident in their protein structure. In view of the enormous significance of this fact to the possible mode of operation of genes, it is advisable to restate the modern line of approach here. It is based upon what may be termed the 'template' hypothesis. Just as a metal master template is employed in the production of thousands of plastic records of a piece of music, so there may be a replicator of proteins within the organism. *DNA* has been cast for the role of living template (page 394). Bacteria exposed to a solution of *DNA* obtained from a different type of bacterium proceeded to synthesise a different type of protein, having absorbed some of the *DNA* supplied. But it has also been shown that the artificial removal of nuclei from cells does not destroy their ability to synthesise protein. Reference has already been made (page 394) to ribonucleic acid (*RNA*). This is present mainly in the cytoplasm and nucleoli, where it exists in the form of dense particles. It is probable that *RNA* molecules are parts of *DNA* molecules, transferred from the nuclei. In the cytoplasm they appear to hold amino-acids in line in specific sequences. These amino-acids are released, condensing to form polypeptides, at the same time as the single-stranded *RNA* molecules combine to form double helices through the pairing of compatible bases, as occurs in *DNA* molecules (see below). Replication of *RNA* molecules follows the same pattern as that of *DNA*. A single *DNA* molecule consists of chains of desoxyribose (sugar) molecules, linked together by phosphate groups and with a base attached to each. The bases involved are adenine, thymine, guanine and cytosine, referred to as *A*, *T*, *G* and *C* respectively. A small portion of such a molecule may be represented thus:



There is an immensely wide variation of ratios and sequences of the bases concerned, but the numbers of *A* and *T* on the one hand and of *G* and *C* on the other are always equal. Every molecule, in fact, takes the form of two chains wound around each other, through thousands of turns, about a common axis. The chains are united by pairs of rods, formed by pairs of the bases, *A* pairing only with *T*, and *G* with *C*. For replication, the chains unwind and each half acquires its natural complement, determined by the limitations of base-pairings. The necessary raw materials must, of course, be present in the nucleus, and a supply of energy is required. There may be as many as four thousand such units in a single *DNA* molecule, giving it a molecular weight of anything up to ten

million. Such a molecule probably represents a series of genes. It should be noted that, in *RNA*, the base thymine (*T*) is replaced by urocil (*U*).

RNA may be regarded as 'messenger' molecules, conveying instructions from *DNA* for the synthesis of specific proteins. Alternatively, the roles of *DNA* and *RNA* may be likened to those of architect and contractor respectively. For further information on this subject the reader is referred to *Cells and Cell Structure*, by Dr E. H. Mercer (Hutchinson Educational).

Every gene, through the physico-chemical effects it exerts during development, is believed to be primarily responsible for the appearance of a particular character. It has recently been suggested by Adolf Butenandt (in *Endeavour*, published by I.C.I.) that there are three possibilities concerning the mode of action of genes –

(1) The gene may possess the properties of an enzyme and catalyse gene-linked reactions (i.e. those chemically governed by gene-substances).

(2) The gene may form an enzyme as a primary or secondary product.

(3) The gene may control enzyme activity – e.g. by the production of specific activators or inhibitors.

In spite of the structural concept of continuity of heredity material throughout the chromosome, there is still much justification for regarding genes as functional units in linear array. But it is not to be assumed that the individual gene plays no part in the regulation of other characters, or that its effect is entirely independent of the other genes with which it is in company. The final result of development is an expression of the sum-total of the influences of all the genes acting as one collective whole. The total of genes together constitutes the **gene-complex**, or **genome**, differing for almost every individual. This would be expected, since, so far as is known, many genes have at least one alternative (allelomorph), so that the number of possible combinations of genes is extremely large. As will be seen in Chapter 35, it is the gene-complex which is of such great evolutionary significance.

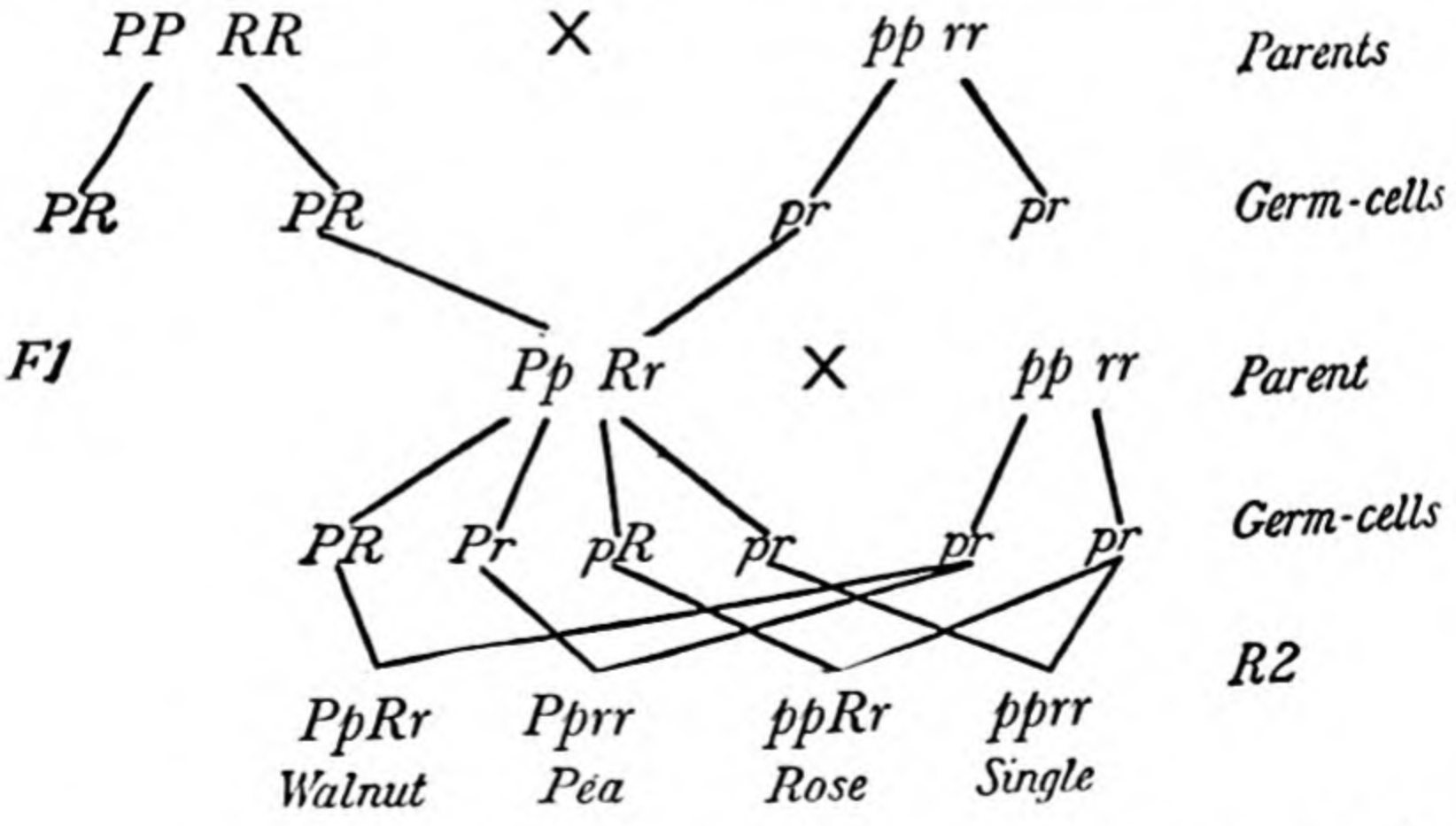
By a study of the cross-over values between selected genes, maps of chromosomes have been constructed, showing the genes in sequence. For example, considering the genes *A*, *B* and *C*, it is found that the cross-over value between *A* and *C* is equal to the sum of the cross-over values between *A* and *B*, and *B* and *C*. This is accounted for on the assumption that the genes are borne in straight lines on the chromosomes, in this case in the sequence *A*, *B*, *C*, assuming that breakage is equally possible at any point on the chromatids involved, for in this event the only factor determining the probability of breakage between *A* and *B*, for example, is the distance between *A* and *B*. The problem is complicated, however, by the fact that, not infrequently, double crossing-over occurs, and thus genes, separated as a result of one breakage and reunion, will become associated again by the same events at another chiasma between the same pair of chromatids. Furthermore, the formation of a chiasma between

two spirally-coiled chromatids (as they are at meiotic prophase) appears to reduce the possibility of further chiasma formation in the immediate vicinity, probably by limiting mechanical strain. All these factors have to be taken into account by the genetical expert in the construction of chromosome maps.

Complementary Genes

So far it has been assumed that definable characteristics are the result of the expression of a single dominant gene in the body-cells of the organism in question (ignoring for the present the homozygous recessive condition). Thus, grey body in *Drosophila* is due to the presence of the gene *B*. But there are many instances of characters being produced by the interaction of *two* dominant genes. Such genes are said to be **complementary** and the following example will serve to illustrate the principle involved.

When pure-bred poultry with single combs are crossed with pure-bred poultry with walnut combs all the offspring have walnut combs. When members of this *F*1 generation are mated with the pure-bred (recessive) single-combed variety, pea-, rose-, walnut- and single-combed birds are produced in equal numbers. This can be explained on the assumption that the genes responsible for pea-combs and rose-combs are dominants, represented by *P* and *R* respectively: their inoperative allelomorphs are represented by *p* and *r*. When *P* and *R* appear together the result is a walnut comb, whilst the absence of both *P* and *R* causes the formation of a single comb. Thus the crosses instanced may be tabulated as follows –



A further example is provided by the inheritance of pigmentation in mice. Here a basic gene for pigment-formation must be present before

either one of two genes – one for wild type, or agouti, which is dominant, and one for black (its recessive allelomorph) – can influence the *type* of pigmentation.

Dominance and Recessiveness

So far the impression has been created that, when two contrasting allelomorphs are present, one of them is totally dominant, expressing itself fully, whilst the other is completely recessive. This is, in fact, not invariably the case, for on occasions *both* genes exert some influence upon the final result. The following example will serve to illustrate this principle of partial dominance. An unusual physical defect in the human frame manifests itself in the presence of relatively short fingers. A recorded case of marriage between two Norwegian cousins, both with this defect, reports that a child of the union showed extensive malformation of the skeleton and did not survive infancy. These facts can be explained on the assumption that the parents were both heterozygotes for the gene responsible, its effects being restricted by the other allelomorph present. In the homozygous condition it proved fatal in early life. In other words, the gene in question expresses itself *partially* in the heterozygous condition, and is therefore not fully dominant. Similarly, in a Swedish family a dwarf and deformed child resulted from the union of two parents, themselves of less than average height and with short limbs. Again it is to be assumed that the parents were heterozygotes in which the effects of the harmful gene were reduced, whereas in the child this gene was present in the homozygous condition.

Further examples of the absence of true dominance may be drawn from poultry and from cattle. Thus, a black Andalusian fowl, crossed with a splashed white, produces offspring with a bluish plumage. A cross between a red Shorthorn and a white one produces a 'roan', in which both red and white hairs are to be found.

Multiple Allelomorphs

So far it has been tacitly assumed that every gene may be represented by either one of two alternatives – e.g. the gene for body-colour in *Drosophila* may be that for grey colour or that for black. This is by no means always true, for in many cases there are three or more possibilities. Such are **multiple allelomorphs**, which may be defined as a series of three or more genes, any one of which may be present at a specified locus on either member of a pair of homologus chromosomes and all of which are responsible for controlling the development of a particular characteristic. Two examples will make this concept clear. Thus in Man there are four allelomorphs in the series concerned with the determination of blood groups (page 358). Wherever such a series exists there is usually a sequence of dominance and this is well illustrated here. Thus the genes in question are labelled for convenience in accordance with the

antigens for the formation of which they are responsible – i.e. *A*1, *A*2, *B* and *O* (no antigens). This means that there are ten possible genotypes for an individual in respect of these genes, namely *A*1*A*1, *A*2*A*2, *BB* and *OO* (all homozygotes and hence producing the corresponding phenotypes) and also the heterozygotes *A*1*A*2, *A*1*B*, *A*1*O*, *A*2*B*, *A*2*O* and *BO*. It is important to note that *A*1, *A*2 and *B* are all dominant to *O*, so that, for example, the genotype *A*1*O* gives the phenotype *A*1 and the genotype *BO* the phenotype *B*. Where either *A*1 or *A*2 occurs together with *B* the phenotype is mixed *A*1*B* or *A*2*B* (such persons are universal recipients). But the genotype *A*1*A*2 yields the phenotype *A*1, indicative of dominance. Thus *A*1 and *B* seem to be equally potent, as it were – i.e. neither is dominant to the other – whereas *A*1 is dominant to *A*2. All three (*A*1, *A*2 and *B*) are dominant to *O*, which may be regarded as a somewhat inert gene.

A second example is concerned with the chemical composition of haemoglobin. This substance appears to vary in composition in different parts of the world and it has been conclusively demonstrated that the discrepancies are due to the particular amino-acid incorporated in the haemoglobin molecule. In most cases this is glutamic acid, but commonly amongst native Africans, for example, this is substituted by the alternative, valine. Numerous other variations are known, each presumably initiated by the presence of a particular member of a multiple allelomorphic series. Where the gene for normal haemoglobin (containing glutamic acid) is present in the heterozygous condition, the majority, but by no means all, of the corpuscles appear to contain the normal pigment, thus providing yet another example of incomplete dominance.

Such considerations as the above caused Dr Penrose in his recent book, *Outline of Human Genetics* (Heinemann), to liken genes to cards upon which are written instructions to be followed out during the process of development. Thus, in the above example, the 'normal' gene gives directions for the making of glutamic acid, and the other allelomorphs for different amino-acids as substitutes. When any gene-pair is heterozygous one set of instructions may be followed implicitly and the other ignored. This would represent the state of affairs when one member of the pair of genes was totally dominant and the other totally recessive. Where the result is a compromise between two sets of instructions, partial dominance is observed. This analogy facilitates a ready appreciation of the phenomenon.

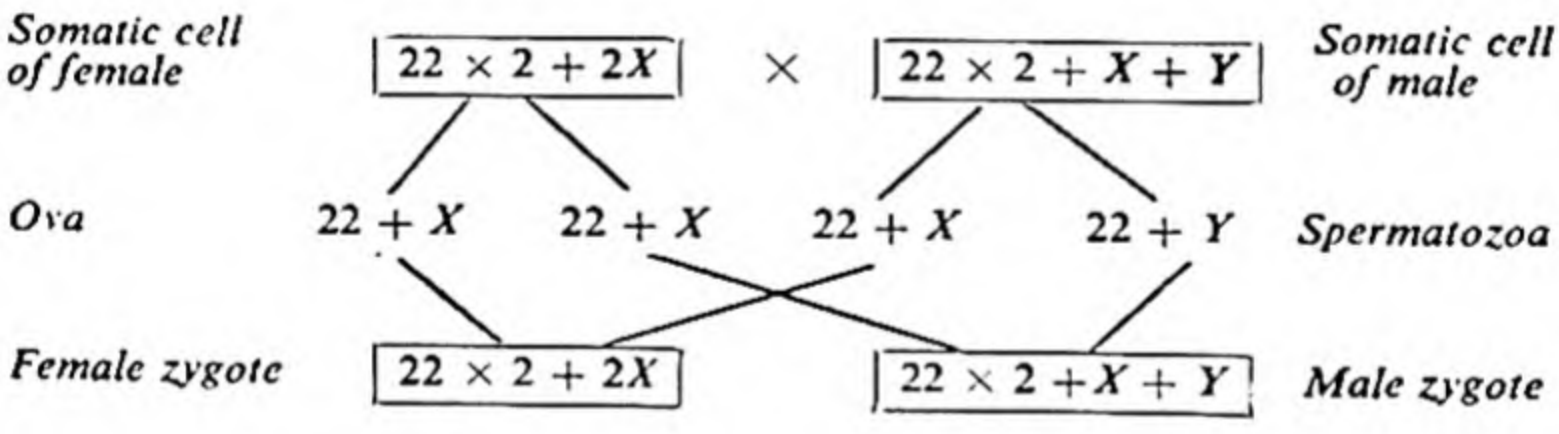
Determination of Sex

This may best be illustrated by means of a definite example. In man there are twenty-three pairs of chromosomes, twenty-two of which are identical in male and female, and are termed **autosomes**. The remaining pair in the female consists of two similar chromosomes, known as the **X-chromosomes**. In the male there is one chromosome similar to the

X-chromosome of the female and called by the same name, whilst its partner is smaller and of different shape. It is called the **Y-chromosome.** The two *X*-chromosomes in the female and the *X*- and *Y*-chromosomes in the male are styled the **sex-chromosomes.** When a primary oöcyte becomes an egg there is reduction in chromosome-number, so that every egg contains 22 autosomes and 1 *X*-chromosome. But in the male two kinds of spermatozoön may be formed, each containing 22 autosomes, but one carrying with them an *X*-chromosome and the other a *Y*-chromosome. When an egg is fertilised by an *X*-containing sperm the total is brought up to 22 pairs of autosomes and 2 *X*-chromosomes. Thus the zygote becomes a female. With a *Y*-containing sperm, on the other hand, the zygote has the constitution 22 pairs of autosomes, *plus* an *X*-chromosome *plus* a *Y*-chromosome, and thus becomes male. These facts may be represented in the figure on page 583.

This further explains why males and females are conceived in approximately equal numbers, on the assumption that the two types of spermatozoön are equally active.

Since the two sex-chromosomes in women are identical (*XX*), the female sex is here said to be **homogametic**, for every egg-cell produced must contain an *X*-chromosome. Since two types of spermatozoön are formed, containing respectively an *X*- and a *Y*-chromosome, the male is the **heterogametic** sex. This is the condition most commonly found in higher animals, but in Lepidoptera and birds, as well as in some fish, Amphibia and reptiles, the female is heterogametic.

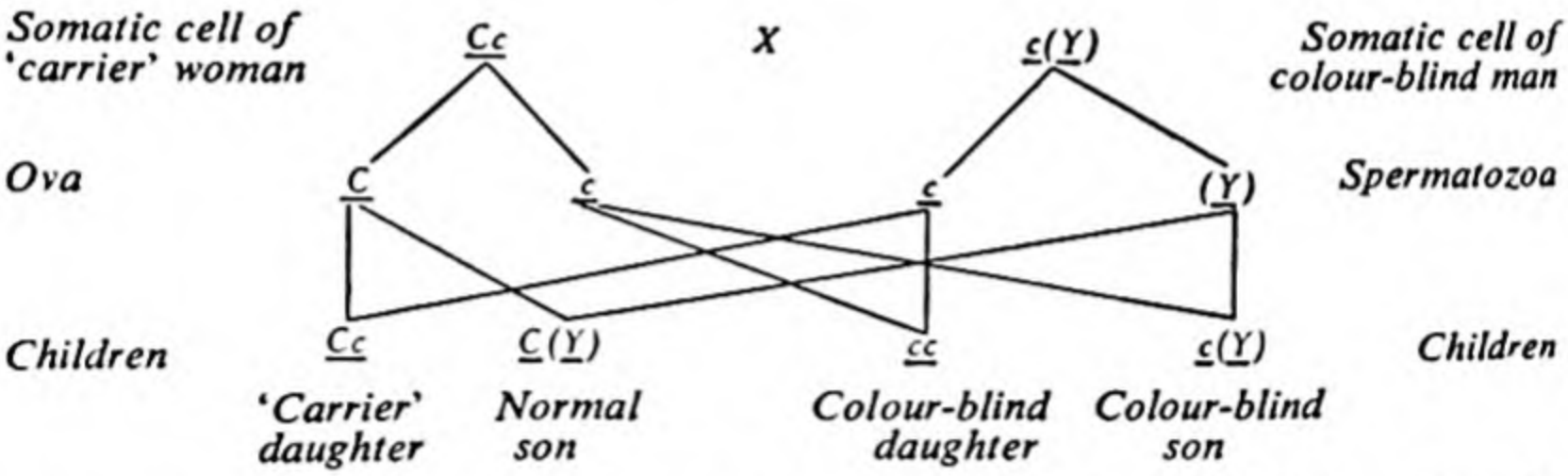


A few other points of interest will be dealt with briefly, exhaustive treatment being impracticable at this stage. Thus factors borne on the sex-chromosomes must have particular distribution amongst the sexes. This phenomenon is termed **sex-linkage**, and affords further evidence for the chromosome theory of sex-inheritance. An example occurring in the human being will serve to make the general principles clear. Colour-blindness is of very rare occurrence in women, but considerably commoner in men. It is believed that the gene responsible – an allelomorph of the one imparting normal powers of vision, to which it is recessive – is borne on the X-chromosome. Thus the genetic constitution of the sexes in respect of this factor may be as follows, where *c* represent-

the gene for colour-blindness, *C* that for normal vision and (*Y*) the ineffective *Y*-chromosome of the male.

Colour-blind woman	*cc*	Colour-blind man	*c* (*Y*)
'Carrier' woman	*Cc*		
Norman woman	*CC*	Normal man	*C* (*Y*)

The results of breeding between the various categories may now be readily worked out, and below is given one example – a 'carrier' woman with a colour-blind man.



It will, of course, be apparent that colour-blindness will be of much rarer occurrence in women than in men, for, whereas *one* gene for colour-blindness is sufficient to impart this defective characteristic to a man, two such genes must be present for the same effect to be produced in a woman.

It is also interesting to note that sons *must* derive their gene for colour-blindness from their mothers, since the *Y*-chromosome, essential to maleness, must be derived from the fathers. Thus a colour-blind man cannot have colour-blind sons unless his wife is at least a 'carrier'.

In contrast with sex-linkage, discussed above, some somatic characters are described as **sex-limited**, or **sex-influenced**. Amongst these may be mentioned stature, head-size and baldness. Baldness in man is not sex-linked in the manner described above, nor is it due to a gene on the *Y*-chromosome. The gene for baldness is autosomal, but the extent of its expression depends upon the sex-hormones, those of women being unfavourable to it. The same is true for the other examples quoted above. Thus the group of genes responsible for stature in general operates more vigorously in the physiological environment provided by males. This is characteristically true of mammals as a whole. Thus bulls are customarily recognised from a safe distance by their so formidable physique.

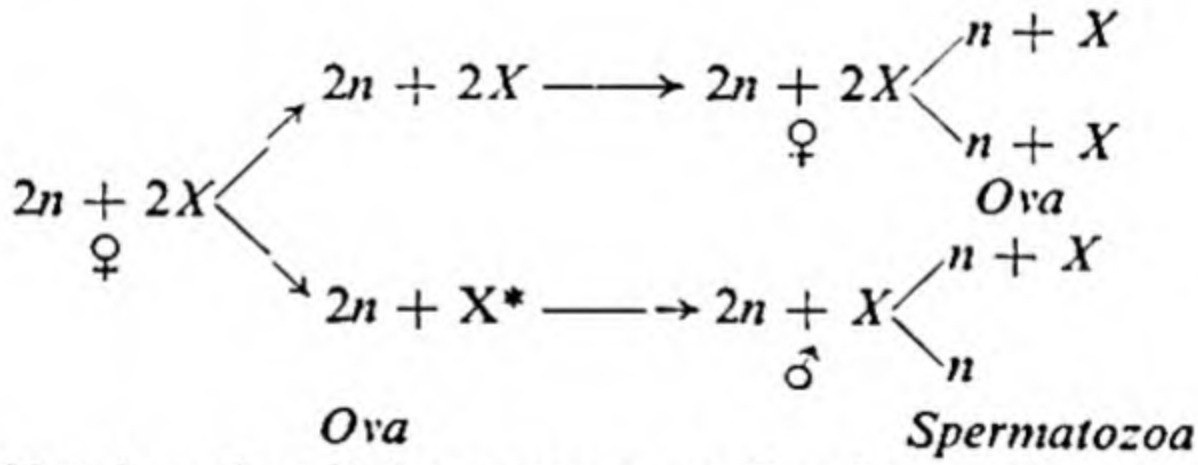
Parthenogenesis

Closely associated with sex is the phenomenon, particularly prevalent amongst insects, of parthenogenesis, whereby generations of female offspring are produced without recourse to fertilisation of the eggs liberated. Such is of some advantage in a number of ways. Thus it leads to rapid

multiplication in favourable conditions and eliminates mating problems. Successive generations, all consisting of potential mothers, are formed. By itself, however, it has not found evolutionary favour, for it precludes the formation of new gene-complexes, and hence eliminates variability. It is therefore common to find parthenogenesis and sexual reproduction associated in a cycle of propagatory activity. There are two distinct types of parthenogenesis, classified according to the behaviour of the chromosomes. They are –

(*a*) *Diploid.* Here the ova contain the diploid number of chromosomes and develop into further generations of parthenogenetic females and ultimately into sexual forms (male and female), the chromosome-content of whose germ-cells is reduced to the haploid condition. This is characteristically the case with aphids, where the male has no counterpart at all to one of the *X*-chromosomes of the female – i.e. no *Y*-chromosome is present. It has been suggested that in an ovum destined to develop parthenogenetically into a male there is at least a partial loss of one of the *X*-chromosomes during meiosis. This state of affairs may be represented diagrammatically as follows, where $2n$ stands for the diploid number of autosomes –

$$2n + 2X \underset{\text{♀}}{\longrightarrow} \underset{\text{Ova}}{2n + 2X} \xrightarrow{\text{Parthenogenesis}} \underset{\text{More ♀s}}{2n + 2X}$$



* Note loss of an *X*-chromosome, as referred to in the text.

(*b*) *Haploid.* In this case the females are diploid in respect of their somatic cells, whilst the males are haploid. All eggs contain the haploid number of chromosomes, with the result that those which develop parthenogenetically become males, whilst those which are fertilised become females. The best known example of haploid parthenogenesis occurs in the life-history of the honey bee.

Polyploidy

This abnormal state of affairs involves the occurrence of sets of chromosomes in numbers greater than the diploid. Thus some or all of the body-cells of an animal may contain three (triploid) or four (tetraploid) sets. In general this phenomenon is much commoner amongst plants than in

the animal kingdom. There are two distinct varieties of organism manifesting polyploidy. Thus –

(*a*) *Autopolyploids.* Here there occurs a doubling of chromosome number (i.e. tetraploids) in organisms otherwise normal in appearance and fertility. In such tetraploids it is common, in the zygotene stage of meiosis (page 316) for all homologous chromosomes to associate intimately together and to segregate irregularly at metaphase. In consequence there is much infertility.

(*b*) *Allopolyploids.* These are typically the result of duplication of chromosomes in hybrids. The two diploid sets of chromosomes from different parents are usually not perfectly matched, whilst the organisms themselves are roughly intermediate in character between ancestral forms. Chromosomes usually associate in simple pairs at the zygotene stage of meiosis, with the result that they segregate normally, giving a high degree of fertility.

Heterothallism

This is normally controlled by a series of multiple allelomorphs, fusion being prevented when two like genes are present. In *Coprinus lagopus* (a toadstool) there exists a double series of genes, with the result that successful zygospore formation is likely to occur in only 25% of cases. This is apparent from a study of the following table, where the operative genes are denoted as *A*, *B*, *a*, *b*, so that a haploid nucleus engaged in fusion can contain only one member of each pair.

	AB	*Ab*	*aB*	*ab*
AB	−	−	−	+
Ab	−	−	+	−
aB	−	+	−	−
ab	+	−	−	−

In all squares except those marked + at least one gene will be duplicated in the zygotic nuclei, and zygospore formation will consequently fail.

Physiological Incompatibility

The problem of physiological incompatibility, whereby the pollen grains of certain plants fail to effect fertilisation following their transfer to the stigma of a flower of the same plant, and in some cases a partial failure where closely-related varieties are employed, has been largely

investigated in the Sweet Cherry, *Prunus avium*, of which many varieties are known. In this plant self-pollination invariably fails, whilst the results of cross-pollination between varieties are inconsistent. Sometimes it is completely successful, sometimes partially so, and at other times a total

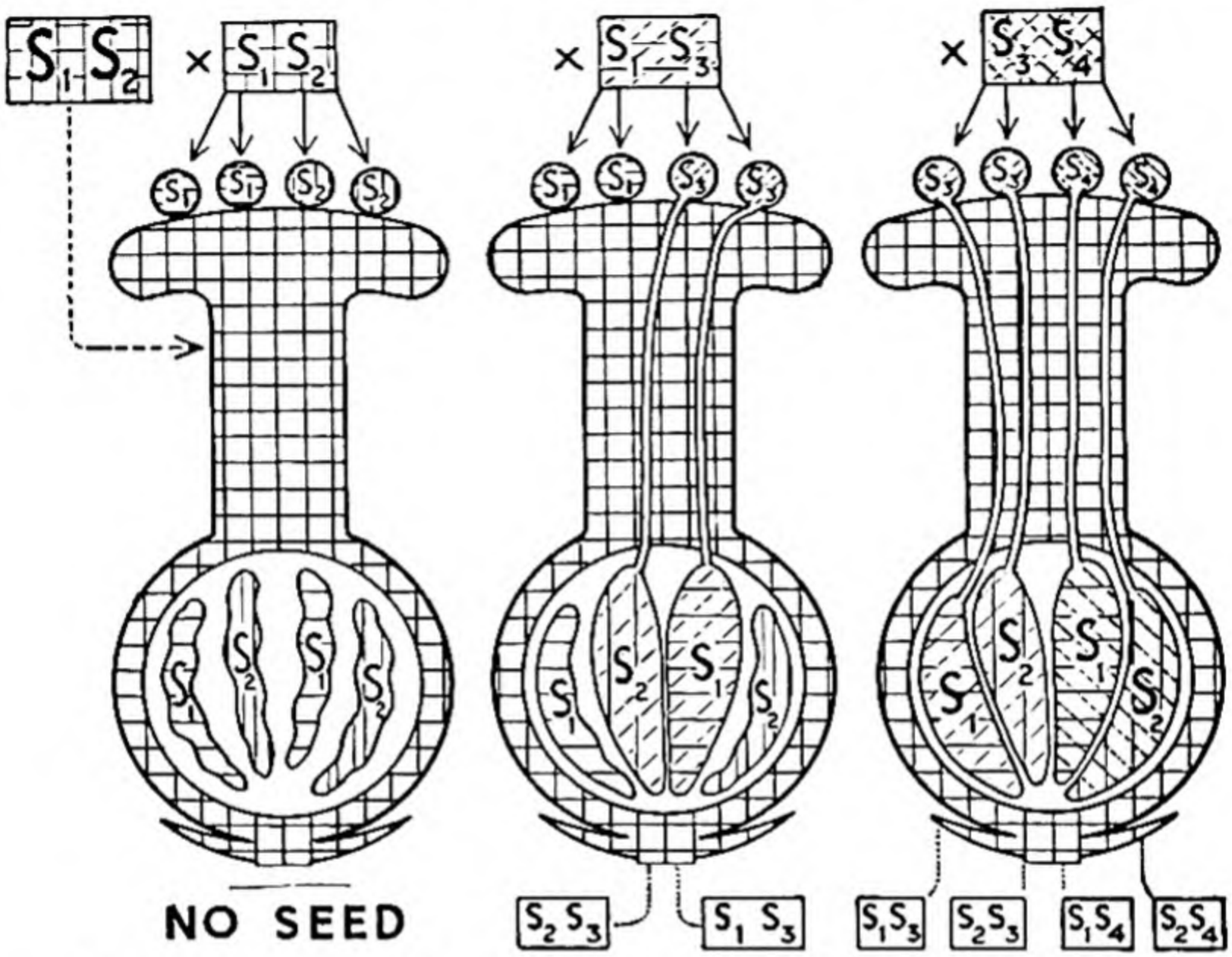


FIG. 329 – Diagram showing the physiological relationship between pollen and style and the genetic relationship between parent and offspring with homomorphic incompatibility. S_1S_2 styles receive, (i) self or similar pollen on the left and their ovules remain unfertilised; (ii) in the centre mixed pollen, part of which, if in sufficient quantity, can fertilise all ovules, and (iii) on the right wholly compatible pollen, all of which can fertilise the ovules.

NOTE. – No progeny can be incompatible with their mother, but in the middle case a half will be incompatible with their father.
(From *The Elements of Genetics*, by C. D. Darlington and K. Mather. Allen and Unwin.)

failure. It was early realised that the failure to induce fertilisation resulted from the very slow growth of the pollen tube, so much so that it never reached the micropyles of the ovules. Clearly, then, the incompatibility exists between the pollen grains and the tissues of the style. This state of affairs is now explicable on a genetical basis. It is dependent, in fact, upon a multiple allelomorphic series, and if the same representative occurs in the pollen grain (haploid) as is borne on one member of the chromosome pair in the cells of the style (diploid), then incompatibility

results. A study of the accompanying diagram will help to make this conception clear. Members of the allelomorphic series are represented as S_1, S_2, S_3, S_4, whilst it is to be further assumed that the genetic constitution of the cells of the style is in every case S_1S_2. Thus in the first case no seeds will be formed, since each pollen grain carries either an S_1 or an S_2. In the second case pollen grain carrying S_1, will be incompatible but those carrying S_3 will induce seed-formation. As a matter of practical significance this probably means that *all* the egg-cells will become fertilised, since pollen grains are normally greatly in excess of ovules, and there will be sufficient S_3 pollen grains for total fertilisation, in spite of the failure of the S_1 variety. In the final example all the grains are compatible, so that any ovule may co-operate with any pollen grain in the production of a seed.

It is estimated that in the Sweet Cherry there must be at least twenty genes in this multiple allelomorphic series, and the fact that incompatible pollen grows even more slowly than usual when the temperature is raised indicates that the genes must be responsible for a positive blocking action, and do not merely exert a negative influence.

Cytoplasmic Inheritance

In the foregoing pages the genes have been depicted as the sole controllers of the inheritance of specific characteristics. In conclusion it is necessary to note that certain facts of inheritance are explicable only on the assumption that an important part is sometimes played by the cytoplasm in this respect. Two definite examples will serve to illustrate this point.

HEREDITY IN PARAMECIUM. Sonneborn discovered that two races of *P. aurelia* co-exist. They are styled the 'killers' and the 'sensitives', on account of the fact that the former exude a poison which kills the latter. Their respective characteristics are hereditary. Thus, in conjugation between two members of opposite races, the progeny are 'killers' if the 'killer' parent provides the cytoplasm – i.e., if the migratory nucleus (see page 12) passes from the 'sensitive' parent into the 'killer' – and 'sensitives' if the cytoplasm is derived from the 'sensitive' parent. If conjugation is prolonged and there is visible exchange of cytoplasm, as well as of nuclei, between the conjugants, then all the offspring are 'killers'. But nuclear factors are also involved. 'Killers' are believed to contain a dominant gene, *K*, in either homozygous or heterozygous state. If, by selective conjugation, this gene is replaced by the recessive allelomorph, *k*, the capacity to kill is gradually lost. Once lost, it cannot be recovered by the re-introduction of *K* to the stock, which continues indefinitely to produce 'sensitives'. Thus it would appear that the ability of the gene *K* to express itself depends upon the nature of the cytoplasm of the individual. The cytoplasmic factor is termed *kappa* and has been identified with actual particles present in the cytoplasm. There are twice as many

of these particles in individuals with the *KK* genotype as in those with the *Kk*, whilst they are absent from the homozygous recessive individuals (*kk*). Speculation on the nature of Kappa particles seems to lead to the conclusion that they are better regarded as plasma genes, rather than as infective bodies.

There is here an excellent example of interaction between genes and cytoplasm. It may well be that, in cellular organisms, the differences between the cells of an individual are due to the influence of the cytoplasm, which is itself more susceptible to environmental conditions, determining what genes shall operate in different parts of the body during development.

PIN- AND THRUM-EYED PRIMROSES. Heterostyly in *Primula* has already been referred to (page 278). The fact that legitimate unions between thrum and pin give a high rate of seed production, whilst the illegitimate (thrum *X* thrum, or pin *X* pin) gives a much lower fertility, suggests that this is merely another case of incompatibility. But an explanation solely in terms of genes is inadequate, since *all* the pollen from any one plant behaves similarly. The thrum plant in nature is heterozygous, containing the dominant gene, *S*, and its recessive allelomorph, *s*. Pin plants are homozygous recessives. Infertility of illegitimate unions is due to the blocking of the growth of the pollen tubes, as in the case of the Sweet Cherry. Yet the behaviour of pollen grains containing the gene *s* depends upon the pin or thrum nature of the parent plant which produces them. In the diagram above, all four types of mating are indicated – the legitimate (*A* and *C*) and the illegitimate (*B* and *D*).

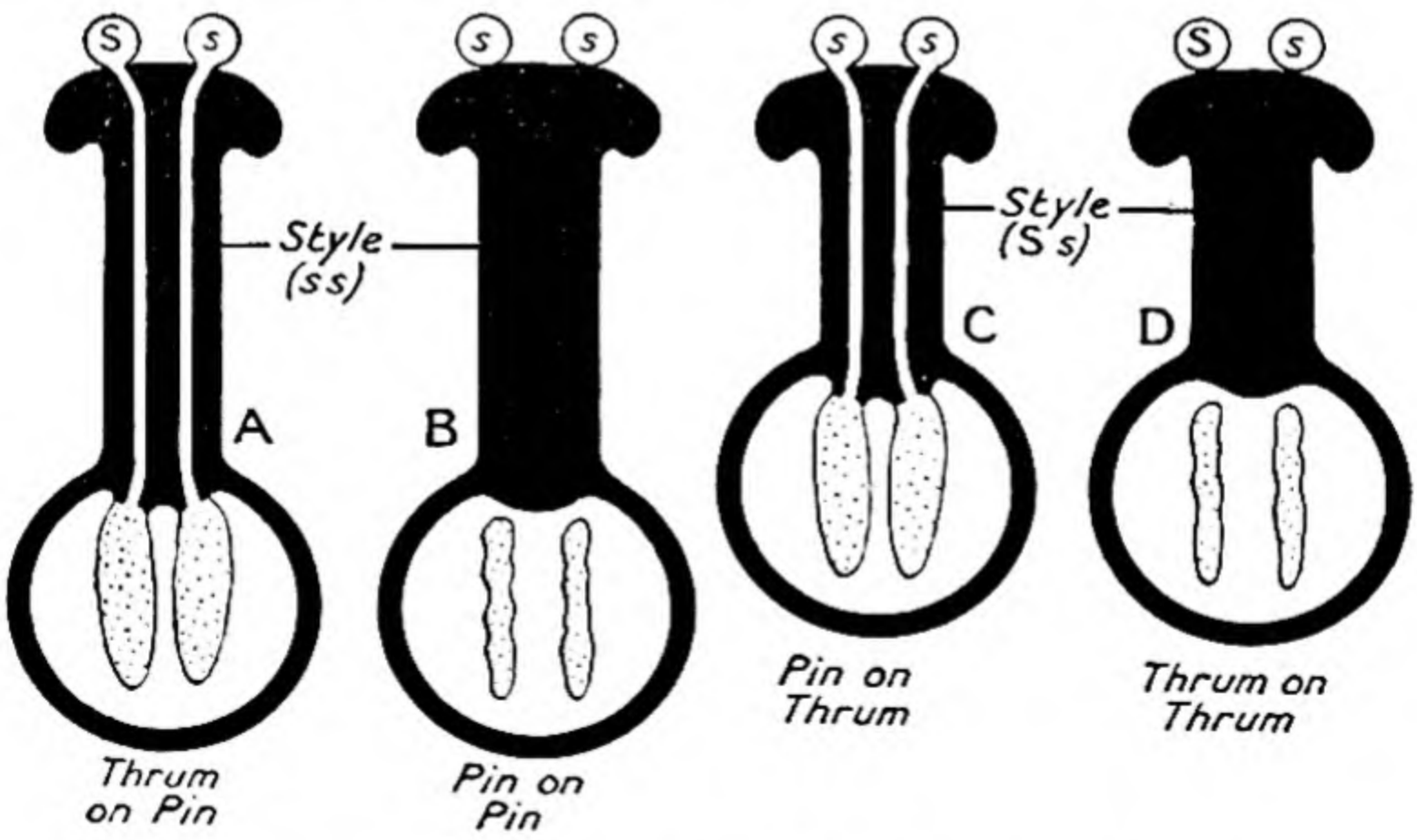


FIG. 330 – Diagram to show the usual behaviour of thrum and pin pollen on the stigmas of the two types of Primrose.

Thus in *A*, *s* pollen grains germinate successfully, whilst in *B* they do not, in spite of the fact that the cells of the style are in both cases of the genetic constitution *ss*. It is therefore to be assumed that their behaviour is predetermined by the cytoplasm of the plant which bears them.

PLASTID INHERITANCE. Perhaps one of the best examples of a stable system of hereditarily transmitted particles outside the nucleus is provided by plastid inheritance in plants. A peculiar character of pigmentation has been found to occur in a wide variety of genera; it is the 'albomaculatus' leaf variegation, in which the normally green leaf shows irregular patches of lighter green or white. At its maximum the entire leaf may be devoid of chlorophyll. It varies in distrubution from part of a single leaf to all the leaves upon a substantial branch. Irrespective of the source of the pollen, it is found that seeds formed from flowers on wholly green branches give rise to normal plants, seeds from flowers on branches with variegated leaves to mixed offspring (green, variegated and white in no fixed proportion) and seeds from flowers on branches whose leaves are white to white-leaved plants. It would appear that a system exists for the transmission of chloroplast primordia through the cytoplasm of the egg-cell. Such a system is termed a **plastome**. The total absence of these primordia from a branch rudiment would account for white leaves throughout, whereas their local absence in otherwise normal leaves would lead to variegation. Such idiosyncrasies of development are more likely to be attributable to cytoplasmic influence than to nuclear factors, since the behaviour of genes is known to be so remarkably consistent.

. . . . .

Although many of the topics dealt with in the foregoing pages have received only superficial treatment, it is hoped that the student will have acquired an elementary knowledge of the principles involved, and that the interest awakened may result in further reading of the subject.

CHAPTER 34

Evidence for Evolution

The theory of organic evolution, postulating the progressive change in form of animals and plants from very elementary beginnings, is to be sharply contrasted with the dogma of special creation, implying the creation of animals and plants which have, since the origin of life, exhibited the same diversity of structure as is apparent today. Evolution thus implies changeability of form; special creation implies stability. In the main, therefore, evidence for evolution must be sought along two lines. An attempt must be made to demonstrate this changeability, whilst the descent of one form from another involves fundamental similarities of structure between different groups, and these similarities must be looked for. Corresponding organs may become variously represented, and may even fulfil different functions, but in spite of this a common evolutionary descent may often be traced. The various items of evidence will now be considered in turn.

Palaeontology

Rocks are either volcanic or sedimentary. The latter, as their name implies, are formed by the deposition of sediment in the beds of rivers and the sea. Further deposition results in the compression of the lower layers, which become recognisable as rocks. It occasionally happens that the skeletal remains of animals and plants become covered by sediment prior to putrefaction.

Other methods of fossilisation are known. Dust storms may be instrumental in enclosing the remains of terrestrial animals, as also may volcanic ash. Fossils have also been found in asphalt, itself the result of the evaporation of the more volatile components of natural petroleum. Organisms may possibly become petrified, resulting from their replacement, particle by particle, by mineral matter, such as silica, iron pyrites or calcium carbonate. In general, it is only the hard parts of an animal which can be thus preserved, but occasionally evidence of pre-existing life is to be found in the cast of a footprint or the impression left by a soft-bodied animal. By whatever method, the relics so preserved are termed **fossils**, the study of which is known as **palaeontology**. Not too much information must be expected from this source. The prerequisite conditions for fossilisation are so precise as to be rarely fulfilled. Even the strata of the sedimentary rocks may be disturbed by the thrusting up of mountains, whilst erosion by rivers and glaciation also occurs. Through

palaeontology it is often possible to discover the previous existence of animals and plants no longer surviving or to conclude that organisms existing today had no counterpart in bygone ages. This may be best illustrated by means of examples. It is dealt with first, since it is the nearest approach to direct evidence.

An important group of fossil plants is afforded by the **Pteridospermae** which, like the Cycads (page 602), appear to have affinities with the

FIG. 331 – The fossilised remains of *Archaeornis*, the most primitive fossil bird. (From Parker & Haswell's 'Text-book of Zoology'. Macmillan.)
Among primitive features note the clawed front limbs, presence of teeth and absence of large breastbone.

Pteridophyta and the Spermaphyta. The piecing together of fragmentary information has resulted in the evolution of a fairly exact knowledge of the form and life-history of some members of this group. Taking *Lyginopteris* as an example, this plant had fern-like pinnae, the tips of which bore mega- and micro-sporangia. There appear to have been distinctly differentiated stamens and carpels. The protoxylem occurred more or less embedded in the metaxlyem, essentially a fern characteristic, whilst considerable secondary thickening occurred. The megasporangia and ovules had much the same structure as in the Cycads, whilst the microspores (pollen grains) were probably conveyed to the pollen cavities of the ovules, where fertilisation occurred, presumably as in Cycads. Thus the Pteridospermae, although they exhibit fern-like structure, resemble the Spermaphyta in one very important respect, namely that the microspores germinate only in close contact with the megaspore, thereby facilitating fertilisation, subsequent to which seeds were formed.

Archaeornis, a fossil bird, differed in certain particulars from modern birds. Thus its beak was set with teeth, whilst the vertebral column was extended to form a true tail. The digits of the fore-limb bore claws. All these are essentially reptilian characters, though the preservation of feathers denotes the avian nature of the fossil.

The fossil record is, of course, far from complete. This would be expected, since the vast majority of plants and animals perish in conditions where fossilisation is impossible. Especially is this so since the colonisation of land. But there are instances where the fossil pedigree is exceptionally well preserved, and an example is provided by the ancestral history of the modern horse. The earliest known ancestor was *Eohippus*, in which the fore-feet had four well-developed digits and a fifth represented by a splint-bone. In the hind-feet the first digit had disappeared, whilst the fifth was vestigial. In both fore- and hind-feet the middle digit, which alone eventually survived, was already somewhat enlarged.

Protorohippus, which followed, was a somewhat taller animal and had completely lost the fifth digit of its fore-feet. The next link in the series, *Orohippus*, was yet taller, though its principal advance on earlier conditions was in the matter of its grinding teeth, which were more markedly equine. *Epihippus* showed further development in the same direction. In *Mesohippus* the fore-feet contained only three digits (II, III and IV) and a vestigial fifth, whilst in the hind-foot only digits II, III and IV remained. The series is continued through *Merichippus*, *Protohippus* and *Neohipparion*, all of which were still three-toed, though the lateral digits (II and IV) were mere splint bones. Finally the modern genus, *Equus*, appeared, and the total time involved between the two extremes of *Eohippus* and *Equus* has been estimated to be between five and six million years. During this time, as well as the reduction of lateral digits, there was an increase in height of some fifty inches.

Fossil remains of a group of reptiles known as the Synapsida provide

some link between reptiles and mammals, indicating evolutionary continuity between the two classes. The earliest known representatives of the Synapsida had no false palate (page 150), whilst the ear ossicle was a single bone (homologous with the columella of the frog) and the surface of the lower jaw was covered extensively with membrane-bones, including the articular, which was articulated with the quadrate of the skull. A series of fossil Synapsida shows the progressive development of a false palate. At the same time the membrane-bones of the lower jaw became steadily reduced in number, accompanied by the enlargement of one of them – the dentary. The articular, together with the quadrate of the skull, were released from their function and position, migrating to the middle ear to become intercalated between the stapes (the homologue of the columella) and the tympanum, forming respectively the malleus and the incus. Lower jaw articulation was taken over by the dentary with the squamosal of the skull. Thus the gap between reptiles and mammals is partly bridged.

Palaeontology thus serves to demonstrate changeability of structure and in general it may be noted that fossils in the upper strata of the sedimentary rocks are more like living forms than are those in the lower.

Comparative Anatomy and Physiology

When the structural features of various groups of animals are compared it is found that, in groups manifestly not closely related, organs fulfilling the same function are built on different lines. Examples of this

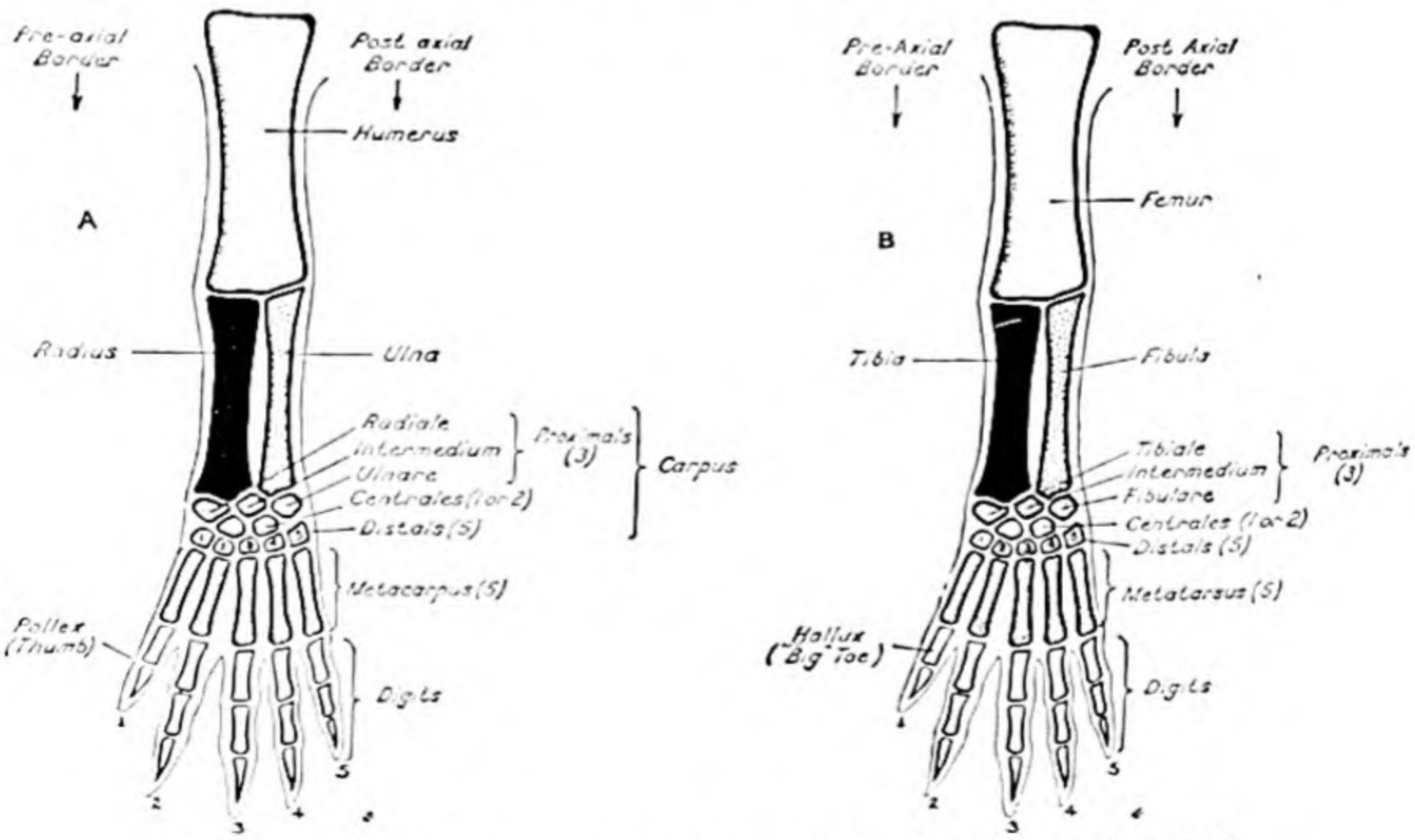


FIG. 332 – The pentadactyl limb. *A.*, Fore-limb; *B.*, Hind-limb.

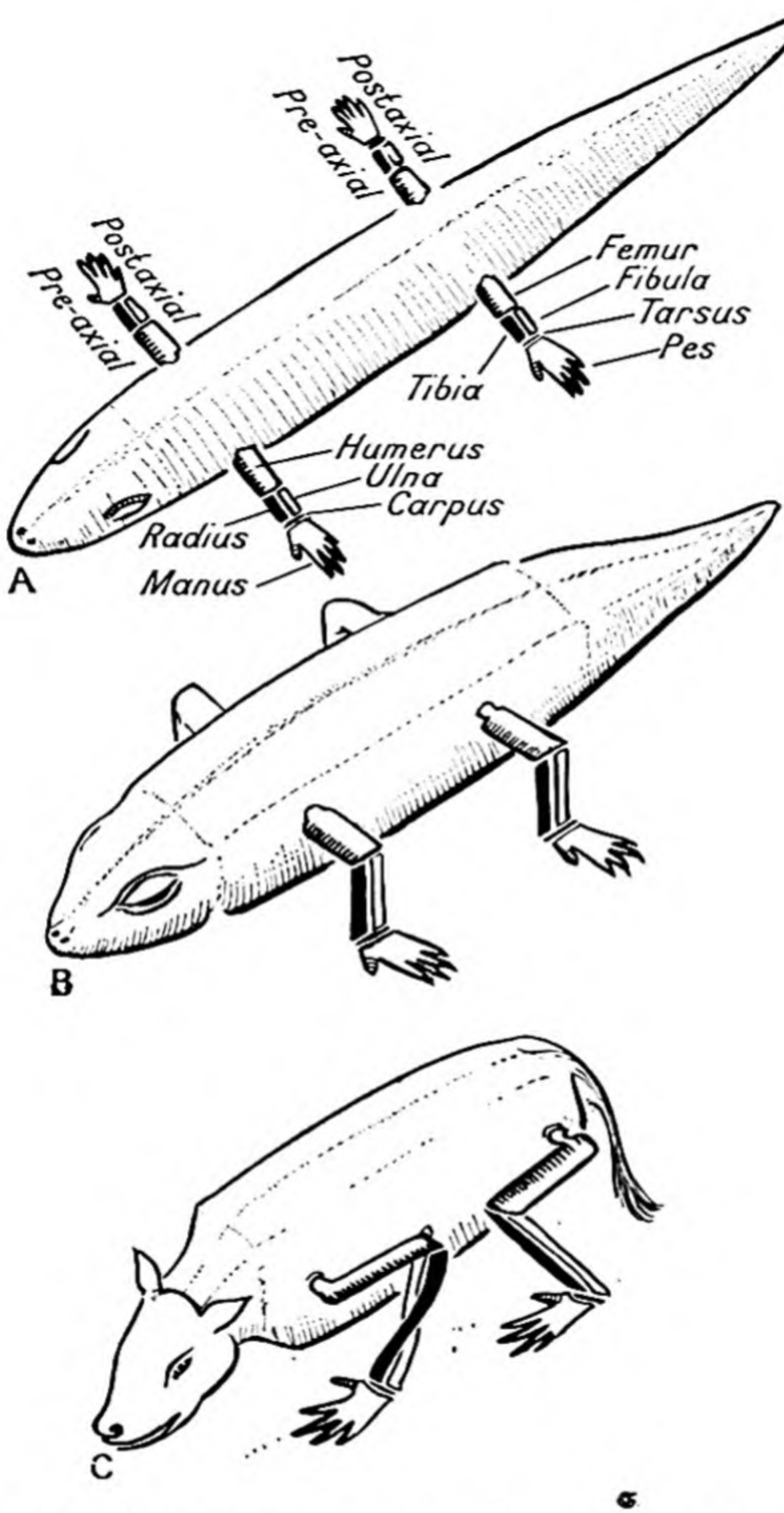


FIG. 333 – Diagram to illustrate the evolution of the Tetrapod limb.

A., Hypothetical ancestral condition; the limbs are at right angles to the body, which rests on the ground; in such a primitive condition the body could only be 'rowed' along

are afforded by the wings of insects and birds and by the walking legs of Arthropoda and mammals. Such structures are said to be **analogous.** In related groups, on the other hand, structures fulfilling different functions are often constructed on a common plan. The pentadactyl limbs of verte-

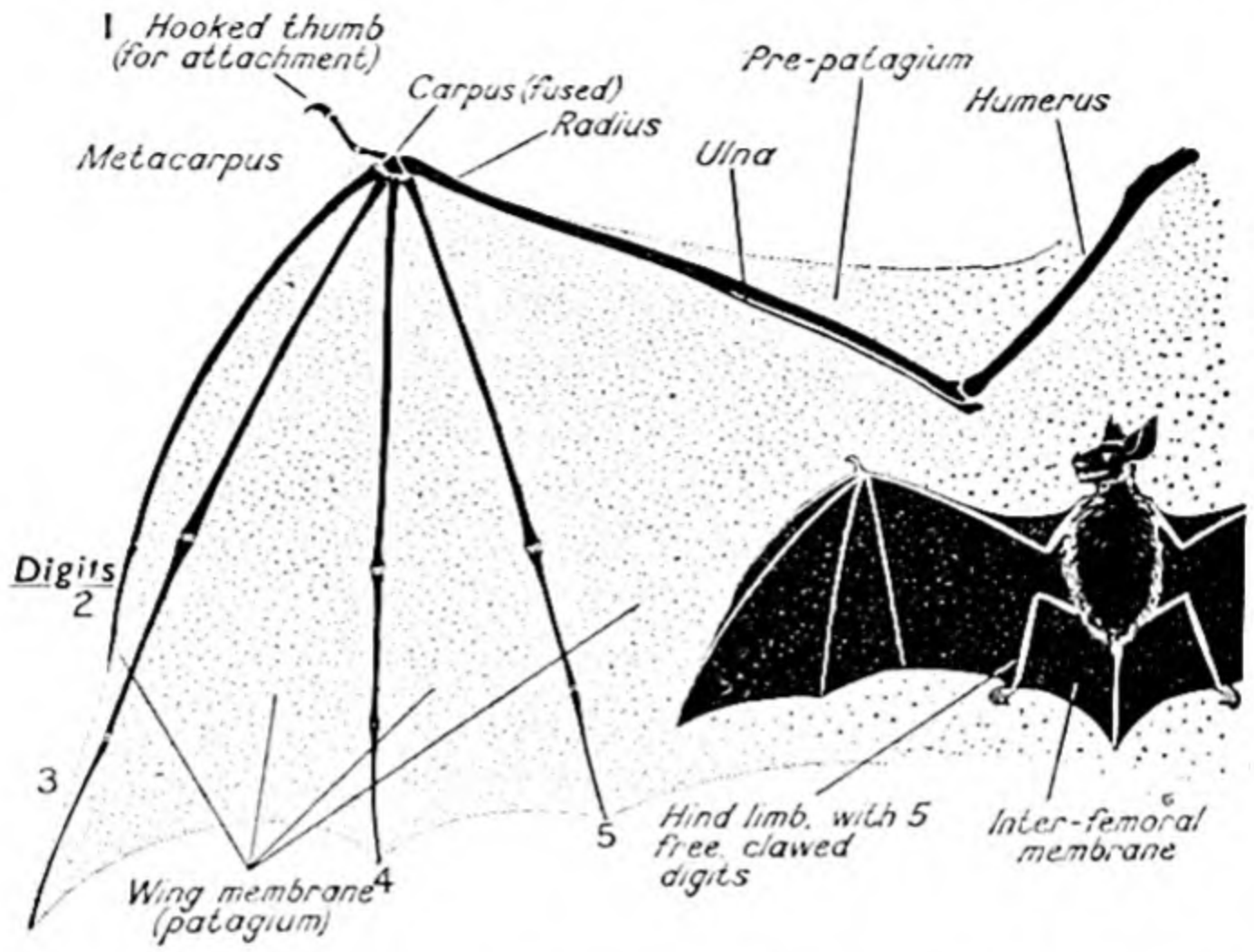


FIG. 334 – Wing of Bat (*Chiroptera*), showing a modification of the pentadactyl limb for flight. The wing is the result of the great elongation of the bones of the hand and the extension of the skin as shown. In the fruit-eating bats there are minor differences.

brates afford an obvious example of this. There are typically present two pairs of limbs, consisting essentially of an upper arm or leg, a fore-arm or lower-leg, a wrist or ankle, a palm or instep and fingers or toes. This basic plan has become modified in the case of the fore-limbs of air-

---

in a clumsy manner. (Note the use of the terms 'pre-axial' and postaxial'.)
B., Note the right-angle bends between the upper and lower limbs and at the wrist and ankle, thus raising the body from the ground and increasing the efficiency of locomotion.
C., The hind-limb is rotated forwards, bringing the pre-axial border to the inside position and the pes pointing forwards. The fore-limb is rotated backwards, bringing the pre-axial border to the outside at its proximal end. This would cause the manus to face backwards, but this is corrected by a forward rotation through 180°. This causes the characteristic rotation of the radius (the pre-axial bone) from its outer proximal position to an inner position at its distal end. The limbs increase in length and efficiency and there is a corresponding reduction in the tail. In mammals this is accompanied by the evolution of a neck.

breathing Vertebrata (Tetrapoda) to fulfil three separate requirements, and consequently the limbs appear superficially dissimilar. In most Amphibia, reptiles and mammals they are accommodated to assist in locomotion on land. A careful study of Fig. 333, with the associated caption, will reveal the way in which the primitive pentadactyl limb has become so well adapted to this end. But in birds the fore-limbs take the form of wings adapted to flight. In mammals further modifications may be discovered. Thus in the bats the fore-limbs take the form of wings, though differing in detail from those of birds (see page 596), whilst in the Cetacea (whales and porpoises), Sirenia and seals the fore-limbs take the form of paddles to accommodate an aquatic mode of life. In turtles it is ob-

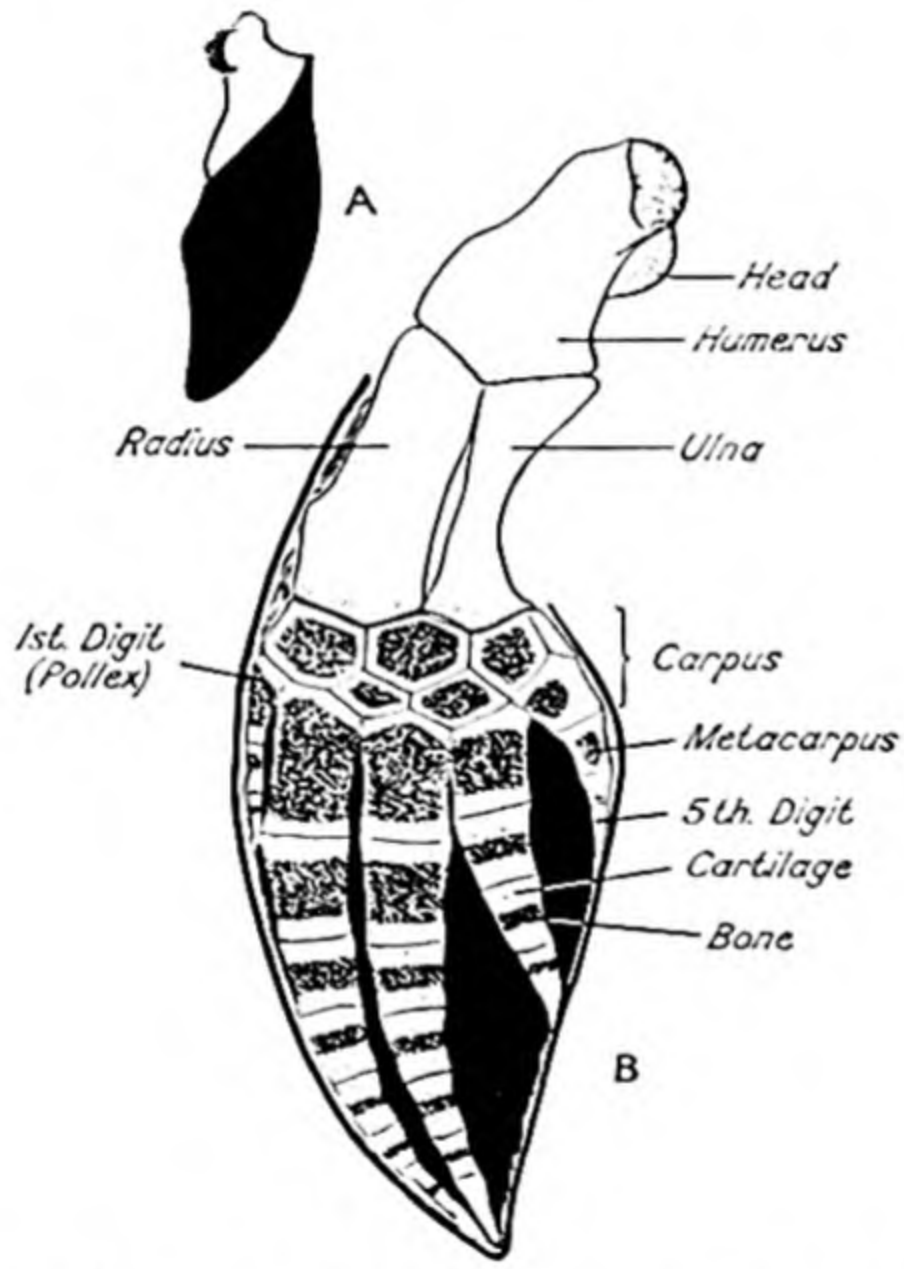


FIG. 335 – Left flipper of a porpoise, dissected to show the skeleton.

served that a similar modification of fore-limb structure has occurred amongst reptiles. But an examination of the skeletal architecture of all these types of limb clearly demonstrates that they are all built on the same fundamental plan, and consequently they are described as **homologous.** Two structures are said to be homologous if they have the same evolutionary history and develop similarly in animals which now possess them. Numerous examples of the phenomenon of homology may be drawn

from the vertebrates and other Chordata. In some fish, notably the Dipnoi, there is a structure, primitively paired, homologous with the lungs of the Tetrapoda. In other bony fish this has lost its connexion with the pharynx and become an air-bladder, concerned with the regulation of the specific gravity of the fish, enabling it to remain at various depths in the water without effort. Considering the Chordata as a whole, a number of structures in *Branchiostoma* may be homologised with superficially dissimilar organs in the Gnathostomata. The endostyle of *Branchiostoma* (page 506) is homologous with the thyroid gland of higher forms, whilst the tongue-bars (page 506) are homologous with the thymus. The mouth of *Branchiostoma* is overhung by a shelf, known as the oral hood. A patch of ciliated tissue, known as the wheel organ, in this region is homologous with the hypophysis of the pituitary body in Gnathostomata. From the discussion of alternation of generations in plants (Chapter 32) the structures homologous amongst various groups will be apparent.

In many groups of animals the last remnants of organs no longer serving any useful purpose are so commonly found that their existence can only be satisfactorily explained on the grounds that they represent the remains of structures once functional in their possessors, the ancestors of surviving forms. Numerous examples of these **vestigial** organs may be discovered amongst vertebrates. Thus in flightless birds – e.g. the kiwi – the wings are very greatly reduced, whilst the nictitating membrane in the inner corner of each eye in man represents the last vestige of the third eye-lid of lower forms. In lampreys and some lizards of the present day, notably the New Zealand tuatara (*Sphenodon*), there is represented a median pineal eye in connexion with the mid-dorsal surface of the brain. It is to be regarded as the remnant of a structure of much greater importance in Amphibia and reptiles now extinct. In higher vertebrates it has become functional as a ductless gland. In man the last vestige of a tail is represented by a coccyx at the base of the vertebral column. In snakes, characterised by the loss of limbs, the pectoral and pelvic girdles are reduced to vestigial form. Vestigial structures are represented amongst plants, and may be exemplified by the minute scales representing leaves in some parastic flowering plants – e.g. the dodder – and by the functionless stamens, termed **staminodes**, occurring, for example, in the figwort.

Comparative Physiology

So far emphasis has been laid on the aspect of structural change in evolution, whilst later attention will be paid to alterations in the course of development. But it is clear that evolution must also have involved the origin of physiological modifications and it is along these lines that evidence for evolution is now to be sought. Again, demonstration of physiological change will be accepted as providing evidence that evolution has occurred.

Perhaps the most convincing investigations of a physiological nature lie in the analysis of the body-fluids of terrestrial animals and those aquatic forms which must be presumed to be related to them through a common ancestry. Not only are the two groups similar in composition, but both resemble sea-water in respect of the concentration of salts in their body-fluids. This is made even more remarkable by the fact that in both cases the amount of magnesium is relatively less, and that of potassium relatively greater, than in modern sea-water, but evidence from geological sources suggests that animal body-fluids resemble in composition sea-water as it was at the time of their origin. With marine animals it would be expected that tissue fluids and the surrounding medium would coincide in composition, for there is often free exchange through a permeable surface. But to maintain this state of affairs in fresh-water and terrestrial animals the evolution of an excretory and osmo-regulatory mechanism is essential. Such must have evolved to make possible the colonisation of these habitats.

Comparative physiology between various members of the Chordata may best be studied in relation to the constitutions of the blood. Chemical methods are not sufficiently refined to discover the differences in constitution between the blood of one animal and another, but a biological method has proved practicable. If the blood of a horse be injected into the blood-vessels of a dog the latter will presently produce a substance which precipitates this foreign blood, in much the same manner as anti-toxins (page 357) are produced for the resistance of disease. The substance formed under these conditions in the blood of the dog may be called anti-horse serum. If this serum be extracted and mixed with the blood of various other animals its effect will be variable. On the blood of a frog or bird it will have no action, whilst it will cause slight precipitation of the blood of a pig and more still with that of an ass. The explanation is that the blood of an ass is chemically more like that of a horse than is that of a pig, whilst that of a pig is more like that of the horse than is the blood of a bird or frog. On grounds of embryology and comparative anatomy the series would be expected to proceed:

Horse – ass – pig – bird or frog,

and this is precisely what occurs in the matter of blood relationships. Similar research with anti-human serum has demonstrated the fact that the blood of the gorilla most closely approximates in chemical composition to that of man.

Further demonstration of the blood-relationship between man and various other animals has been given by determination of the extent to which the latter suffer from essentially human diseases. In general it is found that the more closely are the animals related to man, as decided on grounds of comparative anatomy, the more virulent are the attacks of the disease.

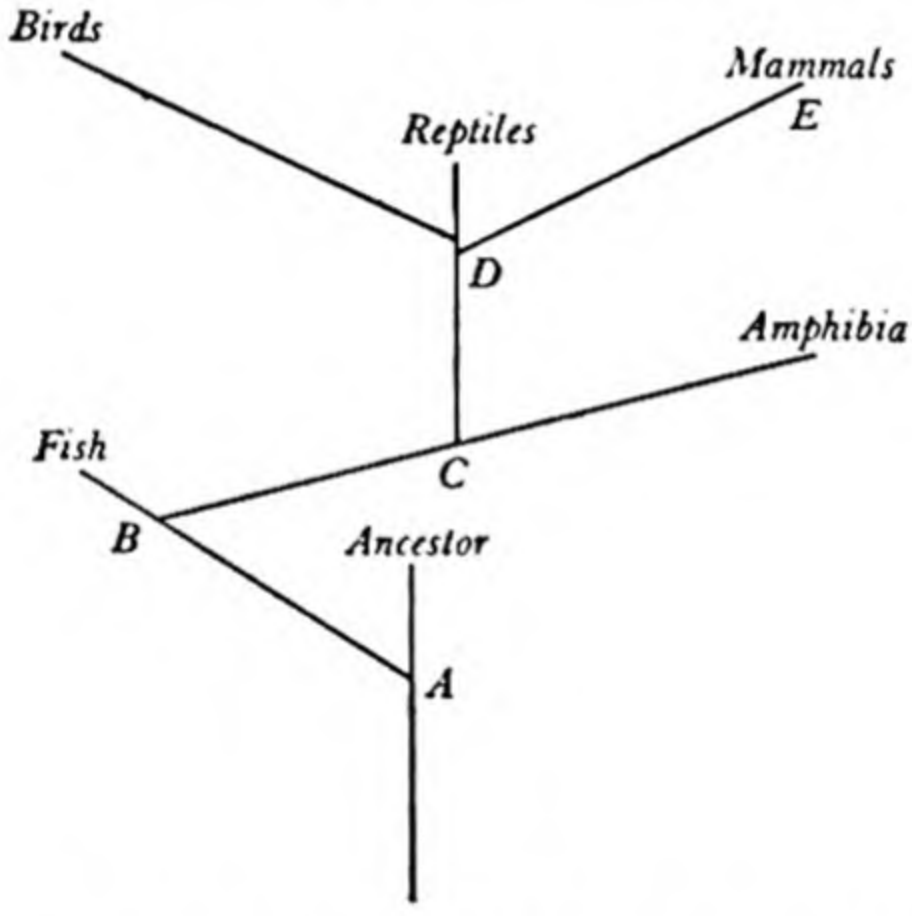
The existence of distinctive blood-groups in man has already been discussed (page 358). Suffice it here to point out that this is indicative of evolution, for it presumably results from the divergence of several lines from a common ancestral point. Also important is the fact that similar blood-groups occur amongst the apes. The most satisfactory explanation of this fact is that both apes and man were derived from a common ancestor.

Evidence from Life-history

The phenomenon of alternation of generations in plants has already been fully described. It is evident that there exists here a gradual transition from Bryophyta to Angiospermae, involving the progressive perfection of the sporophyte generation. This is manifestly in adaptation to colonisation of land by plants. Fertilisation in the Bryophyta and Pteridophyta involves the presence of free water, in which the motile spermatozoids can swim. This is effected by the dwarfing of the generation bearing the reproductive organs. But dissemination of reproductive bodies, as well as access to sunlight for photosynthesis, is obviously favoured by aerial growth, and this is exhibited by the sporophyte, even in the Bryophyta. Accordingly the sporophyte generation assumes priority. But so long as the gametophyte develops independently this is not of very much advantage. Thus the horse-tails and club-mosses are now but a vestige of what they used to be prior to the appearance of the Spermaphyta, for previously they are believed to have colonised the whole surface of the earth in dense, vegetative growth. The Spermaphyta, however, retain the female gametophyte within the body producing it – the ovule. This involves the carriage to it of the microspores, which eventually form the male prothalli. Thus arises the phenomenon of pollination. In the perfected condition the necessity of water for fertilisation has therefore been entirely dispensed with, so that adaptation to life on land is completed. The student will have no difficulty in identifying corresponding stages and structures in the life-history of the principal groups of the plant kingdom.

Embryology of animals provides further evidence. The development of an individual is known as its **ontogeny**, whilst the evolutionary history of its ancestors is termed **phylogeny**. A study of development of individual forms resulted in a statement by von Baer of certain embryological principles. These are – (1) During development, general characters appear before special characters. (2) From the general characters, first the less general, and finally the special, characters are developed. (3) During development, any animal departs progressively from the form of other animals. (4) Embryonic stages of some higher animals resemble the embryonic stages of lower animals, but not the adult form of these latter. Based largely upon these principles came Haeckel's Recapitulation Hypothesis, postulating that every organism, in its ontogeny, recapitu-

lated its phylogeny, or that each climbed anew its genealogical tree. It must be assumed that changes occur, resulting in the origin of one type of animal from an ancestral form. This does not happen merely by the addition of new stages on to the end of the ancestor's completed development, but by some modification during the early phases. Thus, for example, a mammal at no stage resembles an adult reptile, but it does pass through a stage similar to that of the embryo of its reptilian ancestor. Once the embryo of a more advanced form has passed beyond the point of resemblance to the ancestral embryo, then the embryo itself may become significantly adapted to successful development, quite apart from the superiority of the adult to which it gives rise. The formation of foetal membranes by the embryos of reptiles, birds and mammals affords an excellent example of such adaptation. Based on this hypothesis, the following genealogical table may be constructed for the Gnathostomata.



Thus during its ontogeny a mammal may be assumed to travel in order through the points, *A*,*B*,*C*,*D* and *E*, never attaining more than embryonic form of ancestral classes. Rudimentary gill-slits, for example, are formed but are not pierced, the nearest to this condition being found in the Eustachian tube, which survives into adult life. It is homologous with the spiracle of fish.

In many cases the stage-by-stage resemblances between the development of members of different, though fairly closely related, groups is masked by telescoping, and even omissions. Looking at the diagram above, it is as though the mammal, for instance, 'cuts the corners' and makes a more direct journey from *A* to *E* than if it faithfully progressed through *B*, *C* and *D*. Thus, greatly to the individual's advantage, the development period is curtailed. On the other hand, the representation

of an ancestral stage in the life-history of a more advanced group is startlingly exemplified by the presence of a typical chordata larva in the life-history of members of the Urochordata (page 627), as well as by the tadpole stage in that of Amphibia.

Instances of similar developmental phenomena occur amongst plants. Thus *Acacia* is characterised by the possession of phyllodes (page 253), but during its development all stages of transition may be witnessed between pinnate foliage leaves and fully-formed phyllodes.

Intermediate Forms

If every group of the animal and plant kingdoms has originated by evolution from pre-existing groups, there ought to be intermediate stages represented. There are, but extremely few. This might well be expected. The ancestral group is apparently well suited to its environment, even though the new one may eventually be even better adapted. But an intermediate condition may well 'fall between two stools', and consequently would not be expected to survive. One animal is worthy of mention in this connexion. It is *Ornithorhynchus* (duck-billed Platypus). It is found only in Australia where, together with certain other ancient forms – e.g. the kangaroo – it survives owing to the early isolation of this continent, and therefore the loss of competition. It is undoubtedly mammalian, since it has hair and suckles its young. But in the possession of an inter-clavicle in the pectoral girdle and the laying of large, heavily-yolked eggs it exhibits reptilian characters, as is further evident in the absence of separate anal and urino-genital apertures.

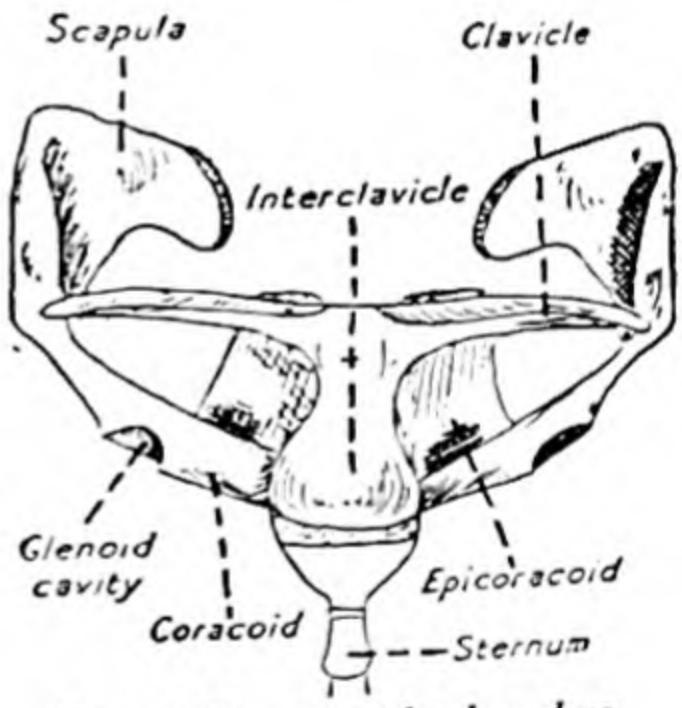


FIG. 336 – *Ornithorhynchus*. Pectoral girdle.

Great care must be applied to the interpretation of such facts. Thus it must not be suggested, for example, that modern mammals have evolved from *Ornithorhynchus*, but instead that both modern mammals and *Ornithorhynchus* have evolved from a common stock. The same consideration applies when interpreting the relationship between *Branchiostoma* and the Chordata. Always it is the common ancestry which must be assumed, and not the direct descent of one from the other. *Branchiostoma* has far too many specialised characters of its own for it to be regarded as an ancestral form.

One group of plants is significant on account of its possession of characters intermediate between the Pteridophyta and the Spermaphyta. Its members are classed as the **Cycads**, to be regarded as relics of a group abundant in the mesozoic epoch, and occurring now only in the tropics.

They resemble palms or tree-ferns in appearance, whilst the leaves are like the characteristic pinnae of ferns. There are numerous vascular strands, in which the protoxylem is within the metaxylem. This is comparable with the condition in ferns, and in marked contrast to the Spermaphyta, where the protoxylem of the root occurs on the outer side of the metaxylem. Secondary thickening occurs in the Cycads. There are present two kinds of spore-bearing organs, corresponding to the carpels and stamens of the Spermaphyta. Each megasporangium (ovule) contains but one megaspore, which, as in the Spermaphyta, is enclosed in a nucellus and integuments, incomplete at one end, forming a micropyle, at the base of which lies a pollen cavity. The pro-stamens bear on their under-surfaces numerous sporangia, within which microspores (pollen grains) are formed. These are borne by wind or insects to the pollen cavities of the megaspores, after which each puts out a short pollen tube. Two spermatozoids are liberated from each pollen grain, and resemble the corresponding structures of lower forms in being flagellate. The megaspore now consists of a mass of tissue, constituting the female prothallus, embedded in which are several archegonia at the micropylar end. In this condition fertilisation occurs, and subsequently only one zygote in an ovule completes development. Soon two cotyledons, a plumule and radicle become differentiated, whilst the residue of the female prothallus constitutes the endosperm. The wall of the ovule becomes modified to form a seed-coat, differentiated into three layers.

Geographical Distribution

A comprehensive study of natural faunas leads to two rather remarkable conclusions. Firstly, places widely separated but with similar climatic conditions possess faunas often strikingly different. This is well exemplified by the British Isles and New Zealand, or by the north and south polar regions. Thus, whereas at the south pole penguins abound but polar bears are unknown, the position is reversed at the north pole. Secondly, members of certain groups of animals are often to be found locally at widely separated points but not in regions between those points. These facts are explicable only on the assumption that evolution has been to some extent a local phenomenon – e.g. new mammalian forms originating in Europe differed from those appearing in Australia. Once new forms have arisen they tend to spread. But there are barriers to their migration, provided, for example, by the sea and mountain ranges. Even if dispersal is successfully accomplished the animals still have to prove themselves adaptable to the environment of their destination. Thus lack of uniformity of animal populations would be expected on such a basis. For example, if penguins gradually evolved from a centre of origin in southern polar regions it would have been manifestly impossible for them to have reached the north pole by any route, although conditions of life there would have proved quite suitable.

The changeability of animal form is made especially evident by a study of island faunas. Islands manifestly impose barriers to distribution of animals, and consequently the evolution which may occur on them is considerably localised. Islands are of two types, namely, oceanic and continental. The former have arisen as a result of land-elevation in the sea, whereas the latter have been produced by separation from a continent. The latter are further subdivided into 'ancient' and 'recent', according to the time at which separation was effected. Only very few animals are able to surmount the barriers to distribution. Thus birds may negotiate the sea by flight, whilst the eggs of insects may be carried across. It is characteristic of ancient groups of animals that they are widely distributed, since such probably occurred prior to the formation of most islands of the present day. Such is exemplified by the Mollusca. The fact that many species of animals which occur on islands are not represented on neighbouring continents is accepted as evidence that on the islands localised evolution has occurred. An example is provided by the insect fauna of St Helena. Twenty-five of the thirty-nine genera of insects occurring there are not found elsewhere. This is explicable on the grounds that no new arrivals of the original stock can reach the island and thus check variation, whilst the struggle for existence may well be so much less severe that forms with useless modifications can survive. Survival of imperfectly adapted forms is evident from a study of the fauna of Australia, for a number of animals – e.g. the kangaroo and the platypus – which survive there occur nowhere else. The suitability of the climate of Australia to placental mammals became clear following the introduction of the rabbit there by man, for it so rapidly established itself as to become a serious pest. The isolation of Australia is believed to be an extremely ancient geological event.

In general the antiquity of a group may be inferred from the extent of its distribution. With more recent groups the distribution is localised. An example of this is provided by fish. Thus the fact that a greater specialisation in structure of fish is found in Ireland than in Britain is accepted as evidence of the fact that Ireland was separated from Britain before the latter lost its connexion with the continent of Europe.

Evolution of Sex

In conclusion it may be well to trace the progressive development of sex in the Protozoa and the simpler Thallophyta. The perfecting of the mechanism of sexual reproduction in higher animals and plants has already been discussed (Chapter 32). In *Copromonas*, found in water frequented by frogs, reproduction normally occurs by binary fission. On occasions syngamy takes place, and to effect this two completely identical individuals fuse to form a zygote. Similar phenomena are observed in *Heteromita*, found in infusions of heads of cod, but here there is slight differentiation between the fusing cells. Each is bi-flagellate, but whereas

one remains attached to the substratum by means of its flagella, the other swims actively upon it. Thus here the differentiation is essentially physiological, motility being characteristic of the male and passivity of the female gamete. In *Coccidium schubergi*, a parasite in the cells lining the intestine of a centipede, *Lithobius*, differentiation is both physiological and morphological. The female gamete is large, passive and distended with reserve food material, whilst the male gametes, formed by the multiple fission of a single cell, each resemble superficially the spermatozoa of higher animals, consisting of little but nucleus, rendered motile by a lashing cytoplasmic tail.

A comparable series amongst the lower plants has already been traced in connexion with the development of the plant soma (page 352). If this is now re-read it will be observed that an evolutionary explanation suggests itself. The sexual process becomes more perfected through the same series. In the Bryophyta and above the progressive development of the sporophyte generation, with the gradual colonisation of land, has already been traced.

Modern Evolution

Evolution must not be regarded as an event of past history. Indeed the origin of a hereditarily stable change in the coloration of certain moths in relatively recent times provides very strong evidence for the process of evolution as a whole. It was observed that, in industrial areas, moths normally exhibiting an off-white colour appeared in ever increasing numbers very much darkened. The survival value of this change was evident, for they were rendered very much less conspicuous to birds, their natural enemies. At first it was assumed that the change was induced afresh in every generation as a result of the contamination of the foliage upon which the caterpillars of the moths fed. That such contamination was indeed responsible for the change was soon verified experimentally, but the more important discovery was made that the new coloration was heritable, being passed from parent to progeny, even if the latter were reared on clean foliage. In other words, a hereditarily stable modification had been induced by changed environmental conditions, or a single step in evolution had been taken.

Conclusion

Apart from the section dealing with comparative anatomy the evidence for evolution has necessarily been treated only very superficially. But enough has been said to demonstrate the essential changeability of form of animals and plants, whilst no reasonable doubt can remain regarding the inter-relationships of various groups. Any attempt to trace backwards the history of life through its manifestation in the form and function of animals and plants must needs fail to attain completeness. Biologists have succeeded in passing progressively farther into the past,

but always there is a point beyond which regress is impossible. That point is continually receding, but never can it vanish. The same applies to speculation of future events, to an even more marked degree, for the postulation of 'things to come' can never be verified unless and until they become actualities. Concrete evidence is often forthcoming for events of the past. But however wide the span of time of which man has, or professes, knowledge, it must always have its boundaries. The mind of man is finite – it cannot comprehend the infinite. The acceptance of the occurrence of organic evolution in no way obviates belief in a Deity, any more than does the acceptance of Avogadro's hypothesis. The biblical account of the creation can be accepted as a poem, and may well be appreciated for its aesthetic value. Biology – the science of life – has become extended in time in an attempt to discover the manifestations of life in the past as well as the present, and what more natural than that relationship between the two should be looked for – and found? The biologist, in fact, may be said to have unrivalled opportunities of discovering some of the ways of his God – the God of Life – but never can this be done to perfection.

CHAPTER 35

Evolution of the Vertebrate Vascular and Urino-genital Systems

In the previous chapter evidence in favour of organic evolution was discussed. There is probably no better method of appreciating the significance of this process than an attempt to trace the history of a set of organs through a number of related types. By this means a conception of the types of evolutionary change, whereby each group has arisen from its predecessor, may be formulated. For this purpose two systems will be selected and their evolutionary history traced upwards from the condition represented in fish to that obtaining in birds and mammals, important intermediate stages being provided by Amphibia and reptiles. Since the anatomy of no reptile or bird has been previously described in the text, a sufficient basis of fact will be supplied as the occasion arises. For the remaining three groups *Scyliorhinus*, *Rana* and *Oryctolagus* will be taken as representative.

Even superficial examination of representatives of the five classes of Gnathostomata (page 629) will indicate a fundamentally similar plan of structure throughout. Thus all are bilaterally symmetrical, metamerically segmented, coelomate Triploblastica, possessing a segmented vertebral column, enclosing a hollow, dorsal nerve-cord, which is expanded and specialised at the anterior end to form a brain, contained within a cranium. For the present chapter the vascular and urino-genital systems will be selected and their evolutionary history traced throughout the Gnathostomata.

Vascular System

This consists fundamentally of four vessels. Lying beneath the alimentary canal is the **subintestinal** vessel, passing forwards. This sends paired branches up the visceral arches to communicate with the lateral dorsal aortae in the body-wall. Posteriorly these two vessels unite to form a median **dorsal aorta**, from which blood is supplied by segmental vessels to the body-wall and by vessels in the mesentery to the gut. Blood from the gut-wall is collected up direct into the **subintestinal** vein, which vessel is interrupted during its passage forwards by the liver diverticulum, in which it breaks up into capillaries to deposit much of its stored carbohydrate material before continuing its journey. De-oxygenated blood from the body-wall is received by a pair of **cardinal** veins, which

are in connexion with the anterior end of the subintestinal vessel by a pair of **ductus Cuvieri**, running in a transverse septum across the coelomic cavity. Primitively there was no specialised heart, for the majority of the vessels were contractile. Keeping the state of affairs in mind, it is possible to trace the development of the heart and main blood-vessels of the various classes of Gnathostomata up to the most highly developed condition found in mammals and birds.

(A) HEART. In the fish the anterior end of the subintestinal vessel has become modified to form a pumping organ, as a result of which the general contractibility of the remaining vessels has been lost. The veins (called sinuses on account of their large size) open into a **sinus venosus**, which communicates with a thin-walled **auricle**. From here blood is passed into a thick-walled **ventricle**, produced forwards to form a contractile **conus**. Running forwards from this is that portion of the subintestinal vessel known as the **ventral aorta**, from which the aortic arches arise. The base of the ventral aorta is swollen to form a **bulbus arteriosus**, distinguishable from the conus in that, whereas the wall of the latter is of cardiac muscle, that of the bulbus is of ordinary involuntary variety.

In the Amphibia, represented by the frog, the auricle has become divided into right and left halves, the former receiving mixed blood from the sinus venosus and the latter oxygenated blood from the lungs. The main artery, the **truncus arteriosus**, is divided transversely by a row of three semilunar valves into a proximal conus and a distal bulbus, whilst it is partially divided longitudinally by a **spiral valve**.

But it is in the Reptilia that the most important differentiation has occurred in respect of the structure of the heart, for this has taken two independent courses. In the group known as the Therapsida the truncus was[1] split into two right down to the base. One of these formed the pulmonary channel, supplying the lungs and opening from the right side of the heart. The other was the systemic arch, and this opened from the left ventricle, the heart itself having become completely divided into right and left auricles and ventricles. This line of evolutionary development culminated in the mammals. Here there is no sinus venosus, this being represented by the sino-auricular node, where heart-beats are initiated and their frequency regulated. The three great veins open independently into the right auricle, whilst the conjoined pulmonary veins open into the left auricle.

The other group of Reptilia, known as the Sauropsida, have become differently specialised in respect of the structure of the heart and their development culminates in the condition obtaining in birds. The truncus has this time become split to its base into three channels, two of which constitute the systemic (right and left) and the third the pulmonary. The two systemic arches cross, so that the right one arises from the left ventricle and the left one originates in common with the pulmonary arch

[1] Note the past tense. No member of this group now survives.

from the right ventricle. In most reptiles the septum between the right and left ventricles is incomplete, but in birds there is no communication between the two ventricles. It will be observed, therefore, that the left systemic arch can distribute only de-oxygenated blood, since it arises with the pulmonary arch from the right ventricle. Accordingly it disappears in birds, where the single persisting systemic arch is the right one, in contrast to the left of mammals. As in mammals, the sinus venosus is represented by the sino-auricular node, whilst in both groups de-oxygenated blood is returned to the right auricle and oxygenated to the left.

(B) ARTERIES. In the primitive condition arteries arise in the form of paired aortic arches from the ventral aorta and pass up the walls separating the visceral pouches. These are the **afferent branchial** arteries. On reaching the gills they break up into capillaries and there the blood becomes oxygenated. This blood is then collected up into a corresponding number of paired **efferent branchial** arteries into a pair of **lateral dorsal aortae**. These pass backwards and unite to form the **dorsal aorta**, distributing blood to all parts of the body behind the pharynx, whilst they are also extended forwards to supply the head. Thus the blood is not returned to the heart after oxygenation, prior to distribution to the tissues, but is carried round the body direct from the gills. Thus only de-oxygenated blood reaches the heart, which is consequently described as 'venous'. This primitive condition obtains in most fish.

In the Amphibia the fish-like circulation is perfectly developed in the larval stages, such as the tadpole of the frog. This is manifestly in adaptation to an aquatic mode of life, but during metamorphosis the arterial system assumes the form suitable for terrestrial existence. Thus it is the supply to and from the gill-slits which must needs be modified, whilst blood must now be distributed to the lungs for oxygenation. The afferent and efferent vessels become directly connected, so that the gills are now circumvented. The aortic arches of the first two visceral arches disappear, though they are never more than transitional. The vessels of the third arches become the carotid arches, being continued forwards to the head as the lateral dorsal aorta of each side. In the frog the vessels of the fourth visceral arch form on either side a systemic arch. These unite with the posterior portions of the lateral dorsal aortae, which two structures join to form a median dorsal aorta. The aortic arches of the fifth visceral arch disappear in *Rana*, though in some Amphibia these, like those of the fourth, form a pair of systemic arches. The arches of the sixth visceral arch become the pulmonary arches, one passing to either lung. The carotid, systemic and pulmonary arches on either side almost always become completely closed off from each other distally, this entailing the loss of intermediate portions of the lateral dorsal aorta. Where such connexions remain, that between the carotid and systemic arches is known as the **ductus caroticus** and that between the systemic and pul-

monary as the **ductus arteriosus**. In birds and mammals the aortic arches of the first, second and fifth visceral arches disappear, whilst those of the third, fourth and sixth become modified, as in the frog, to form the

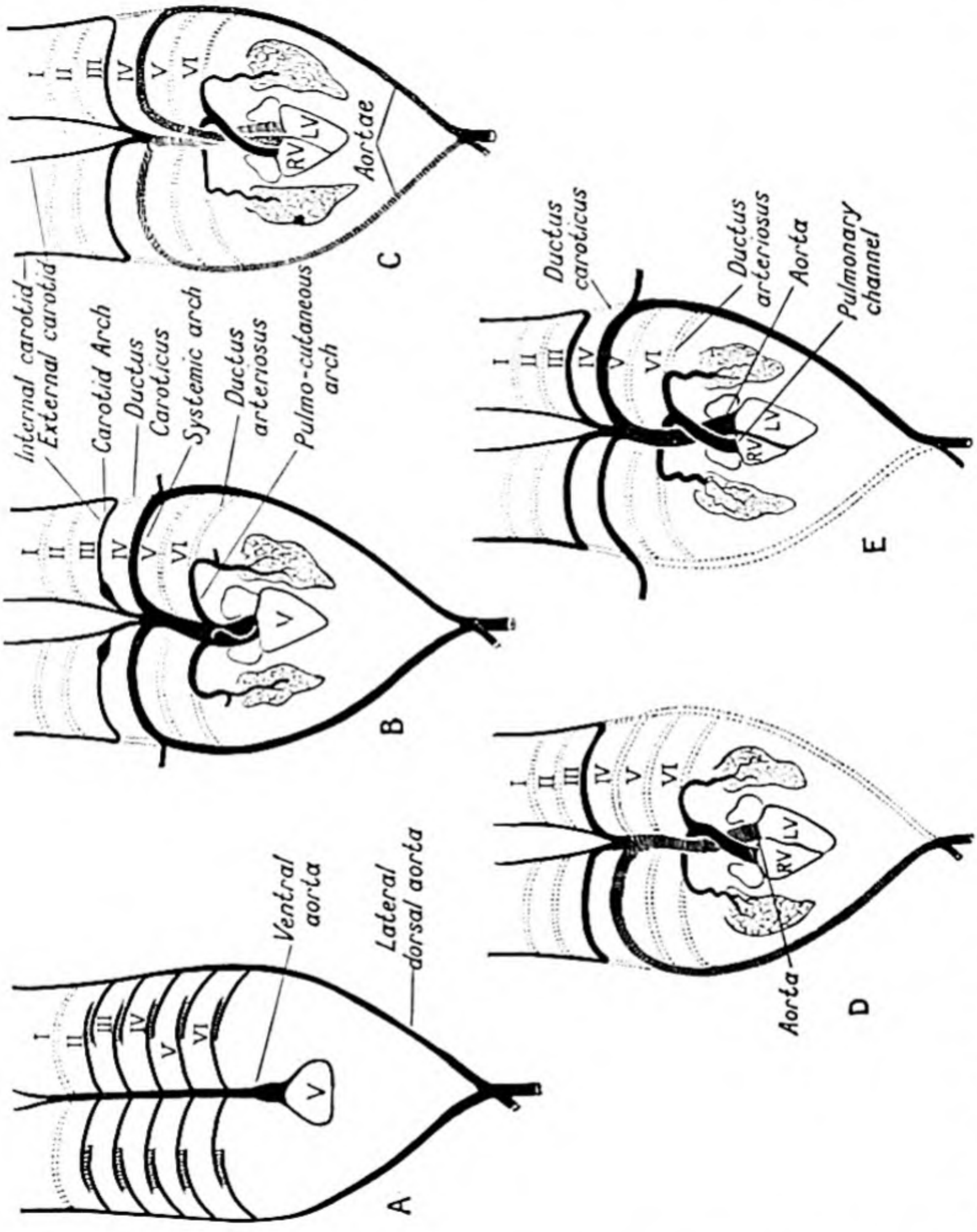


FIG. 337 – Diagrams of arterial arches in *A.*, Fish, *B.*, Frog, *C.*, Sauropsidan reptile, *D.*, Bird, *E.*, Mammal.

carotid, systemic and pulmonary arches respectively. As has already been pointed out the truncus in birds is divided to its base into three channels, the right and left systemic and the pulmonary. The left systemic arch disappears, whilst the two pulmonary arches lead into the pulmonary channel, which itself opens from the right ventricle.

In mammals the systemic arch persists complete only on the left side, whilst the right systemic is represented by the very short **innominate** artery, communicating with the carotid and subclavian of its own side, The left systemic becomes known as the aorta and from it open the carotid and subclavian arteries of that side. The lateral dorsal aorta is preserved on each side in the form of an internal carotid artery to the brain, whilst the anterior extensions of the ventral aorta become the external carotids. These arrangements are made clear in the accompanying figure.

Modifications such as those described above are developed in relation to a terrestrial mode of life, as well as to a complete separation of the heart into right and left sides so that oxygenated and de-oxygenated blood may be kept apart.

(C) VEINS. All de-oxygenated blood is collected up by a number of vessels and returned eventually to the heart. Primitively these consist of a subintestinal vessel to receive blood from the gut, and a pair of cardinal veins draining the body-wall and being in connexion with the anterior end of the subintestinal by a pair of ductus Cuvieri. The subintestinal vein becomes interrupted by the liver diverticulum, so that the portion of this vein on the side of the liver away from the heart is the hepatic portal vein, whilst the hepatic vein carries blood from the liver into the heart. In the fish the arrangement is very similar, whilst two pairs of vessels – the subclavian and the pelvic – are developed for the return of blood from the anterior and posterior limbs respectively. Furthermore, with the development of mesodermal kidneys the posterior cardinal veins become interrupted and break up into capillaries in these organs. The portion of each posterior cardinal vein behind the kidney now becomes known as a renal portal vein. Deep in the body-wall a pair of lateral veins is developed.

In the Amphibia certain further changes have taken place. Thus the anterior portion of the right posterior cardinal vein and the whole of the left have disappeared, whilst a new structure, the posterior vena cava, has been developed to replace them. The only portion of the posterior cardinal vein to persist is the renal portal vein on each side. The lateral veins of the fish have become coalesced in the mid-ventral line in the frog to form the anterior abdominal vein, which now no longer reaches a ductus Cuvieri or the sinus venosus, but leaves the body-wall to penetrate the liver, thus contributing to the formation of the hepatic portal system, the remainder of which is constituted by the hepatic portal vein, homologous with that of the fish. The veins from the hind-legs are also in communication with the renal portal veins.

In mammals the anterior portion of the venous system still remains comparatively unchanged. Posteriorly, however, there is considerable specialisation. Thus the anterior abdominal vein has disappeared, whilst with the development of a metanephric kidney the renal portal system

has been lost. The veins from the hind limbs open direct into the posterior vena cava, the posterior part of which is formed by the fusion of the hind ends of the posterior cardinal veins, whilst the anterior part is homo-

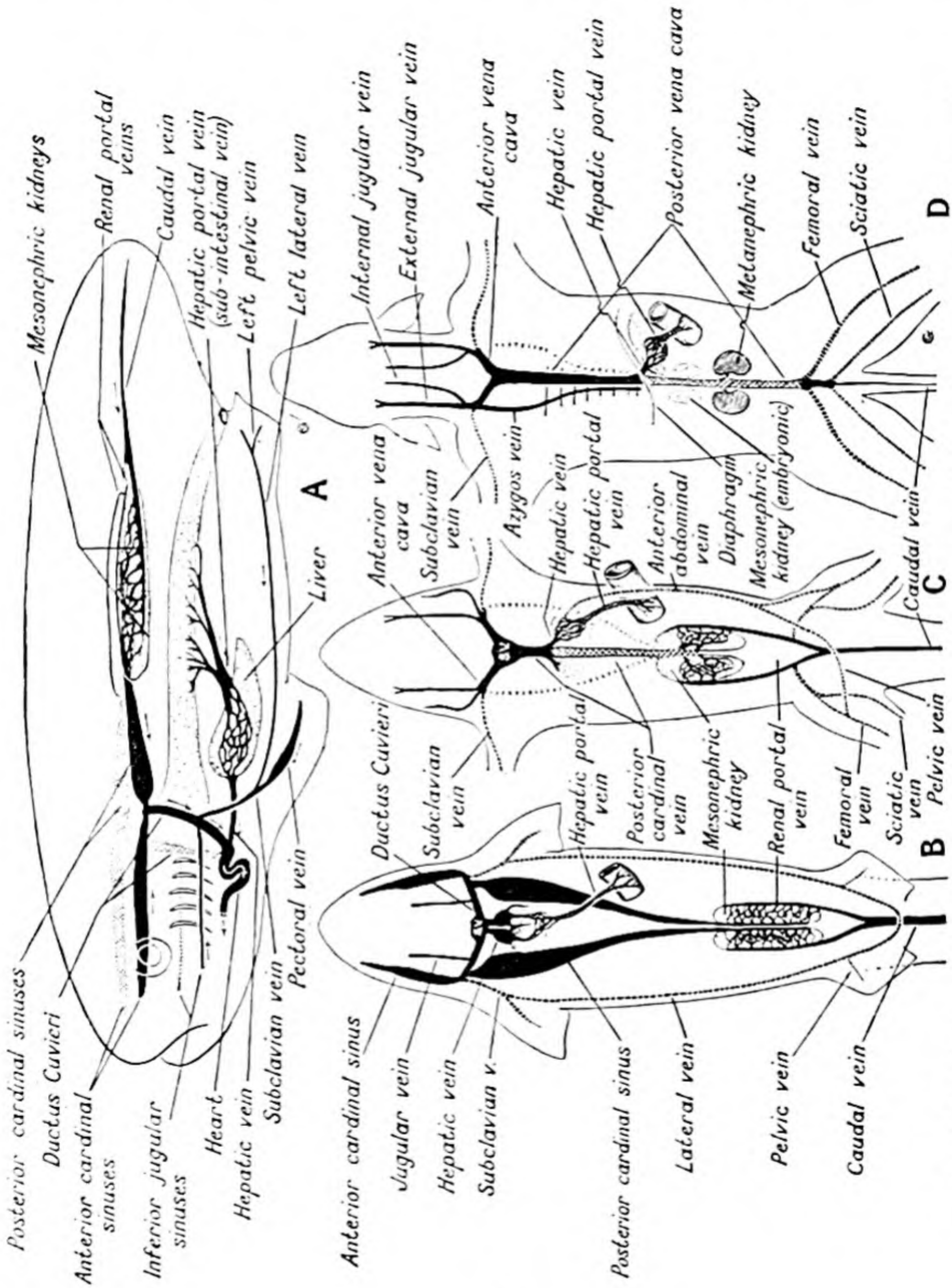


FIG. 338 – Diagrams of vcnous system of *A*., Fish, in lateral view; *B*., Fish; *C*., Amphibia; D., Mammal.

logous with the structure of the same name appearing first in Amphibia. The anterior part of the posterior cardinal vein is represented on the right side by the azygos vein, returning blood from the body-wall in the region of the ribs, receiving inter-costals 5 to 12 from the left side also. This latter vein does not reach the ductus Cuvieri of its own side, but joins the azygos vein. The two ductus Cuvieri become known as the anterior venae cavae.

Urino-genital System

The evolutionary development of this system will be best understood by a description first of all of the origin and development of the kidney in a Chordate prototype, followed by a consideration of the condition of these structures in the various classes of Gnathostomata. Some reference has already been made to this problem in Chapters 6, 7, 8 and 29, but its importance is such as to merit its full statement here.

(A) ORIGIN AND DEVELOPMENT OF THE KIDNEY. The mesodermal pouches of a typical Chordate prototype soon become extended ventrally to enclose the gut in a spacious coelom, bordered by an inner and outer wall. Dorsally, in the region of the nerve-cord and notochord, segmentally-arranged pouches become separated from the ventral coelom by the formation of transverse septa. Connecting each segmental dorsal pouch with the splanchnocoel beneath is a narrow intermediate cell-mass, or **nephrotome**. It is at this stage that development of the kidneys begins. The cavities, known as the **nephrocoels**, of the most anterior nephrotomes establish communications with the coelom by means of coelomic funnels, known as **coelomostomes**, whilst a lateral evagination of the wall of the nephrotome grows towards the body-wall. Meanwhile a rod of mesodermal cells has become cut off from the outer wall of the splanchnocoel (i.e., the somatopleur), and this becomes hollowed out to form a tube, extending backwards as far as the cloaca, with which it communicates. The evaginations of the wall of the nephrotomes open into this tube, so that the coelom is now in connexion with the exterior. The nephrotome tubes now become branched and the blind end of each branch is evaginated to form a **Bowman's capsule** (page 444). Into this passes a branch from the dorsal aorta and one from the cardinal vein, breaking up into capillaries within the capsule to form a glomerulus. The composite structure, capsule *plus* glomerulus, constitutes a **Malpighian corpuscle**. In this way the **pronephros** is formed, and this may be regarded as the functional kidney in the early embryo of our prototype.

Later another set of tubules arises from the nephrotomes some distance posterior to the pronephros. They find the pronephric duct already made for them, and they quickly establish communication with it. Branching occurs as before to form a mass of inter-communicating kidney-tubules, each with its associated glomerulus. This constitutes the **mesonephros**, and the original pronephric duct becomes known as the **Wolffian duct**,

the pronephros disappearing. This mesonephros thus replaces the pronephros as the functional kidney.

Finally a third kidney is developed posterior to the first two. In a manner similar to that already described kidney-tubules are formed, but these do not communicate with the Wolffian duct. Instead a diverticulum arises from the base of this duct and grows forwards. This is the **ureter**. When it reaches the level of this new kidney it sends branches into it, and these eventually communicate with the kidney-tubules, which by this time have become very much subdivided and vascularised. This structure is the **metanephros** and is the functional kidney of the adult in the reptiles, birds and mammals.

(B) FORMATION OF GONADS AND THE ORIGIN OF THEIR DUCTS. The gonads arise similarly in both sexes, though they are quickly differentiated into potential ovaries or testes. Down-growths from the inner ventral corners of each segmental pouch extend some distance into the splanchnocoel, and their walls give rise to the gonads. In embryos destined to become males hollow seminiferous tubules appear in the gonads, and they soon become extended laterally to establish communication with the mesonephric tubules. These composite tubules constitute the **vasa efferentia**, and across them sperms are conveyed to reach the exterior via the Wolffian ducts, known often in this condition as the **vasa deferentia**.

The female makes no use of the Wolffian ducts for the evacuation of eggs. Instead a new rod of cells is split off from the outer face of the somatopleur and this becomes hollow to form a tube, opening into the cloaca near the point of entry of the Wolffian duct. This tube is the **Müllerian duct** and owing to its function of conveying ova to the exterior it is known as the oviduct.

(C) CONDITION OF KIDNEYS AND DUCTS IN VARIOUS GNATHOSTOMATA. In the fish, exemplified by *Scyliorhinus*, the adult kidney is a mesonephros. Excretory products are conveyed to the cloaca by a Wolffian duct on either side. In the male the anterior mesonephric tubules are in connexion with the seminiferous tubules of the testes, thus forming a set of vasa efferentia in relation to each testis and the kidney of the same side. Sperms escape, therefore, via the Wolffian ducts. It is only the posterior portion of the mesonephros which remains actively excretory. The Müllerian ducts in the male are represented anteriorly by a pair of funnels ventral to the oesophagus and posteriorly by a pair of sperm-sacs. In other words, the extremities of the Müllerian ducts persist, whilst their intermediate portions have disappeared. In the female the whole of the mesonephros is excretory and plays no part in the evacuation of genital products. Thus the Wolffian duct persists only for the carriage of urine to the cloaca. But the Müllerian ducts are well developed and function as oviducts, starting as a pair of funnels similar in position to those of the male. It is interesting to note that in *Scylior-*

hinus the coelomostomes remain open, whilst the group to which this animal belongs is further peculiar in that the Müllerian duct arises by a longitudinal constriction of the Wolffian duct.

In the frog, characteristic of the Amphibia, there is little advance on the condition in fish. A pronephros is the functional kidney in the embryo and early larva, but this later becomes replaced by a mesonephros, in connexion with the Wolffian ducts, which serve also for the conveyance of sperms to the exterior. Müllerian ducts arise to function as oviducts in the female, and in the male are represented by the vesiculae seminales (Fig. 93, page 136). The coelomostomes become closed, whilst a ventral evagination from the cloaca forms an urinary bladder. In some Amphibia – e.g., the newt – it is interesting to note that the tubules from the posterior (excretory) end of the mesonephros do not communicate with the Wolffian duct until the latter has almost reached the cloaca. Thus there is here expressed a tendency to separate excretory from genital functions even in the male, and in theory this could be completed if the mesonephric tubules never opened into the Wolffian duct at all, but communicated direct with the cloaca.

In reptiles, birds and mammals the mesonephros is no longer the functional kidney in the adult, its place being taken by the **metanephros**. Its duct, the ureter, is a new structure, formed as an outgrowth from the posterior end of the Wolffian duct and growing forwards to penetrate the tissues of the metanephros. The term 'ureter' should be confined exclusively to this structure and not loosely employed for the urinary channels of lower forms. The condition of the ducts in *Oryctolagus* may be taken as typical of mammals and birds. In the male the mesonephros is represented by the epididymis, partly surrounding the testis. Through the epididymis sperms pass into the vas deferens, which thus represents the Wolffian duct of lower forms. Müllerian ducts are not represented in the male. In the female they are represented by the oviducts, which unite to form a median vagina. The Wolffian ducts disappear completely, though traces of the mesonephros may be found in the form of small patches of tissue, known as the **paroöphoron** and **epoöphoron**.

The above descriptions of comparative anatomy have been given in some detail, since they are so perfectly illustrative of the sort of evolutionary changes which occur during the evolution of a new group from its immediate ancestors. In this, as in all other cases, it must be borne in mind that new groups arise from the more primitive representatives of ancestral forms, rather than from those already specialised to a high degree. Thus, for example, the Dipnoi (lung-fish) are regarded as a specialised group, and, though they possess structures homologous with the lungs of higher forms, they are not on the direct line of tetrapod evolution.

CHAPTER 36

The Mechanism of Evolution

Taking the evidence reviewed in Chapter 34 in favour of the occurrence of organic evolution as conclusive, it remains now briefly to consider the possible explanations which have been advanced to account for the process. The two biologists of primary importance in this respect are Lamarck and Darwin. Their respective views will be shortly stated, after which an outline of the mechanism generally accepted at the present day will be given.

Lamarck

The Lamarckian hypothesis to account for the progress of organic evolution may be summed up in the phrase 'use and disuse'. Briefly, he postulated that any particular organ which was used by a species to an abnormal extent would tend to increase in size, and possibly in complexity. Progressive reduction, either to vestigial form or complete disappearance, was held to be the result of lack of usage of an organ. Such a hypothesis obviously accounts perfectly for adaptation. Indeed it cannot do otherwise, for the environment is essentially the cause of structural change. The animal, if not the plant, to some extent controls its own evolutionary fate by an effort to adapt itself. But it will be seen that this hypothesis makes one fundamental assumption. The result of use or disuse of an organ by a given animal or plant must be expressed as a structural modification in the very early life of its offspring, so that the latter, by its own practice of use or disuse, can further accentuate the change. Such a change in structure occuring during the life-time of an individual organism is known as an acquired character or a phenotypic variation (also page 618). Lamarck's hypothesis depends absolutely on the inheritance of such variations. Experimental evidence has been accumulated to show that such does not, in fact, occur. For example, seventy-six generations of *Drosophila* were retained in total darkness. As a result there appeared to be no diminution in eye-size or modification in response to light. Similarly many breeds of dogs have their tails docked regularly, yet the omission to do this shows that no change has been effected in the hereditary length of the uncut tails. Lamarck considered that the long neck of the giraffe, for example, occurred as a result of progressive increase in length over many generations as a result of reaching to the tops of trees for young foliage. It has been argued that the number of generations of *Drosophila*, for example, dealt with under

experimental conditions is too small to shown any measurable change, and also that in such artificial modification of conditions the essential effort on the part of the animal to adapt itself to its environment is missing. In spite of this defence the hypothesis is not now credited with providing a satisfactory explanation of the progress of organic evolution.

Darwin

Briefly summarised, Darwin's theory supposed the events resulting in the origin of new species to take place as follows. Variations occurred, some of which resulted in the individuals concerned being better equipped, whilst others brought about disadvantageous changes. Following these changes, the environment exerted a 'natural selection'. Those forms less well adapted than their contemporaries succumbed, whilst any advantageous variation was perpetuated and distributed. In other words, the environment came into play following the structural changes, eliminating some in favour of others. Darwin visualised a perpetual 'struggle for existence', resulting in the 'survival of the fittest'. His views are best expressed in the following extract from the concluding paragraph of his *Origin of Species*:

'It is interesting to contemplate a tangled bank, clothed with plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us, these laws, taken in the largest sense, being growth with reproduction, inheritance, which is almost implied by reproduction, variability from the indirect and direct action of the conditions of life, and from use and disuse, a ratio of increase so high as to lead to a struggle for life, and as a consequence to natural selection, entailing divergence of character and the extinction of less improved forms. Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of higher animals, directly follows. . . .'

What might be regarded as the raw materia lof the evolutionary process is provided by variations, for, unless animal and plant form changes, no selection can be applied and thus no progress is possible. It is, therefore, necessary to consider first the phenomenon of variation in rather more detail.

Variation

The term 'variation' is essentially applicable to a process, whereby one individual comes to differ assignably from another. It has become extended to cover not only the process but also the structural discrepancies themselves. Thus variations may be classified, and three schemes

for such are in common use, though they necessarily overlap to a considerable extent.

MERISTIC AND SUBSTANTIVE VARIATIONS. In the first mode of classification variations are grouped according to the actual type of structural modification. **Meristic** variations are concerned with departures from the normal number of repeated parts. Examples are afforded by starfish with four or six arms, instead of the normal five, whilst polydactylism in man is characterised by the presence of additional digits on the hands or feet. **Substantive** variations involve modifications in character of an organ, such as colour, size or shape. Thus the variations by which the members of a human family are normally inter-distinguishable are substantive, including such characters as height, weight, colour of eyes and hair. Many variations are described as physiological. Such may be exemplified by the milk-producing capacity of cows, the egg-laying powers of birds and the number and size of seeds in the pods of a crop of peas. It is highly probable that such are essentially due to modifications in structure – substantive variations – since function can be interpreted only in terms of the form accommodating it.

CONTINUOUS AND DISCONTINUOUS VARIATIONS. In the former category are included narrow departures from the mean condition, showing little tendency to permanent occurrence. They are again, for example, the characters by which members of a human family can be distinguished, and obviously tend to be substantive rather than meristic. Occasionally, however, there is a more spectacular departure from the normal, whilst the unique character of such discontinuous variations extends to their hereditary nature. Thus the Ancon, or otter sheep, appeared as a male member of the progeny of an ewe, differing markedly from its parents in the possession of a longer body and shorter legs. So strong was the inheritance of these peculiarities that this one individual actually became the starting-point of a new breed. Thus continuous variations may well be the result of either the expression of the gene-complex (page 620) of the individuals concerned or the influence of environmental factors on the process of development. Likewise, discontinuous variations, or 'freaks', *may* be similarly explicable, but in those cases where the modified character is hereditary it is clear that chemical or physical changes must have occurred in the substance of one or more of the genes present.

PHENOTYPIC AND GENOTYPIC VARIATIONS. The terms 'phenotype' and 'genotype' have already been explained (page 573). A phenotypic variation is essentially non-heritable, arising during the life-time of an individual. It must be remembered that the life-time begins from the moment of fertilisation of an egg by a sperm, so that in mammals any characteristic acquired by reason of conditions of development *in utero* is a phenotypic variation. A phenotypic variation corresponds to Lamarck's acquired character. But genotypic variations, or mutations,

are basically different, for by their very nature they must be inherited.

A mutation may best be defined as the inception of a heritable variation. It involves a change in the chromosomal constitution of the germ-cells of an individual, so that such is bound to be transferred to the progeny. Naturally-occuring mutations are too infrequent to provide material for research, so that the majority of them have been induced experimentally. The most successful work has been accomplished in *Drosophila* by the subjection of selected individuals to X-rays. Most of the modifications occurring were found to be of the type which occurred naturally, so that the effect of the rays seemed to be to increase the mutation-rate. On some occasions a single gene appeared to have been affected, whilst in other instances a number of neighbouring genes were modified. Where only one gene was changed a **point-mutation** was said to have occurred, whilst a **line-mutation** involved the modification of a number of genes. In either case the result was attributed to the direct action of electrons upon the gene or genes. That reversion to the original form often occurred subsequent to experimentation was accepted as evidence that gene-substance was not actually destroyed, but was either modified or inactivated.

It is clear that, in the vast majority of cases, mutations must occur in the germ-cells of the parents of the aberrant forms. It is just conceivably possible that, owing to peculiarities of circumstances, a mutation may occur in a fertilised egg before development commences, but this is exceedingly unlikely. Once it has occurred a mutation is permanent unless chemical or physical reversion of the gene substance occurs.

Although, as already stated, most mutant genes are at first recessive, a few cases where they exhibit dominance are known, some having been recorded in man. This is important not merely in verifying their occurrence, but also in making it possible to estimate the frequency of such events. One example is provided by a condition known as *epiloia*. This may occur in a child of quite normal parents and takes the form of epilepsy and mental retardment, often accompanied by the development of benign tumours in many of the organs of the patient. The fact that such a condition, should it not be sufficiently severe to cause premature death or invalidism, can be transmitted, possibly through a number of generations, is evidence that a mutation is responsible for its appearance. The same occurs in the case of *retinoblastoma*, where a tumour develops on the retina. Even if the life of the patient be saved by the removal of the eye, or should the disease manifest itself only in later life, then children of an affected parent may be similarly afflicted. A statistical study of such phenomena leads to the conclusion that mutations occur between one and five times per hundred thousand genes at the loci concerned. Generalisations must not, however, be made from this. It is reasonable to suppose that other genes may be either more or less stable than these and the mutation rate will vary accordingly.

The Gene-complex (Genome)

In Chapter 33 it was largely inferred that gene-pairs operated more or less independently of all the other gene-pairs present in an individual. Thus wing-length, for example, in *Drosophila* is determined by the genes *V* or *v* present (page 572). This sort of direct inheritance is believed not invariably to be the case. Rather should it be visualised that the complete development of an organism, assuming normal environmental conditions, is the result of the expression of the genes, not entirely as individual units, but rather as one collective whole – i.e. the gene-complex (or **genome**). In the singing of an oratorio every voice in the choir has its contribution to make, but the listener receives the result of their combined activity. If it be imagined that two contraltos travel about the country as guest members of various choirs, the vocal effects produced by these two singers will obviously depend to some extent on the quality of the respective choirs. In some, for instance, their contribution may be rendered virtually ineffective owing to the exceptionally vociferous nature of the basses. In others they may inspire a splendid performance by the contraltos as a whole. At the same time the influence of the various choirs on the performance by the two contraltos themselves is not without reference to the actual qualities of the latter. Thus, if they are 'old hands', with long experience of choral singing, they are less likely to be 'put off their stroke' by other powerful elements in the choir than if they are novices. So it is with the gene complex. Any pair of allelomorphs will to some extent be influenced by the remaining pairs of allelomorphs in the complex in which they find themselves. This may well be especially true where the pair of allelomorphs under consideration is in the heterozygous condition. Thus, if the pair is *Aa*, in some complexes *A* may be totally dominant to *a*, whereas in others the dominance may not be so complete. At the same time a dominant gene, long established in the tradition of the stock, would probably be less influenced by the remainder of the complex than would a mutant gene, new and inexperienced.

The Course of Evolution

Having analysed the factors involved in the evolutionary process, it is now necessary to investigate the way in which they associate to bring about evolution. Let it be imagined that a mutation occurs and that the mutant gene, if it were able to express itself, would confer an advantage upon its possessor in some aspect of competition. Now initially almost all mutant genes are recessive. At the same time the number of possible gene-complexes in any given type of animal or plant stock is almost without limit, even if it be assumed that each gene has only one contrasting allelomorph. Thus if only three pairs of allelomorphs be considered, namely *A* and *a*, *B* and *b*, *C* and *c*, there are twenty-seven possible com-

plexes, such as *AABBCC*, *AaBBCC*, *aaBBCC* and *AABbCC*. Thus when a mutant gene appears in such a stock – e.g. d^{mu} – it can, in the course of subsequent breeding, find itself in any one of twenty-seven possible gene-complexes. When it is realised that the number of gene-pairs in an individual runs into thousands it is apparent that the number of complexes is virtually without limit. It may so happen that some of these complexes are more favourable to d^{mu} than are others, so much so that when d^{mu} and d are present together the former will express itself. It may even be possible for complexes to occur in which d^{mu} suppresses even the 'normal' dominant, D. As this mutant gene is distributed through the stock during many generations the forces of natural selection set to work. They will pick out for survival those forms in which the gene d^{mu} is allowed some freedom of expression, for in these cases advantage will accrue in the struggle for existence. Gradually those gene-complexes without this new and favourable gene, together with those in which its effects are masked, are eliminated, whilst this gene may ultimately become the accepted dominant member of the series. Thus the sequence which started as D (established dominant), d (established recessive to D) and d^{mu} (totally recessive to both D and d) may now become d^{mu}(totally dominant), D (now recessive to d^{mu}) and d (totally recessive orelimin-ated).

One of the objections levelled at the mutation hypothesis as a basis for the explanation of the process of evolution is that, whereas mutations occur sporadically, evolution is a slow and continuous process. These apparent anomalies are easily reconcilable when it is realised that a single mutation is all that is required for evolution to work upon for perhaps hundreds of generations. In normal instances a mutation gives no sign of having occurred, for a mutant gene is almost always recessive and occurs in the germ-cells of the parents of the individual in whose somatic cells it is first present. The process of selection of the gene-complex continues imperceptibly, in the slow and inexorable manner so characteristic of evolution. It leads inevitably to the evolution of dominance of the genes whose expression imparts the most favourable characters to members of the stock. The phrases *Selection of the gene-complex* and *Evolution of dominance* may be held to summarise this concept of the evolutionary mechanism.

Adaptation to Environment

An adaptation may best be defined, in the substantive sense, as *a special form of a general structure*. Once this is appreciated the meaning of the term can then be extended to indicate the abstract condition of harmony existing between organism and environment. A few examples drawn from various levels of the animal kingdom will make these meanings clear.

ADAPTATION IN VERTEBRATES. The most obvious example of

adaptation amongst vertebrates is the possession of the typical pendactyl limb in varied form.Thus it has become modified to form the wings of extinct pterodactyls, birds and bats – the wings of these three groups are all to some extent dissimilar – the ambulatory legs of many Amphibia, reptiles and mammals, and finally the prehensile organs of the Anthropoids. In each case the general structure referred to in the definition is the pentadactyl limb, exhibiting special form in the various groups.

Glands have become modified in adaptation to various purposes. Thus the sweat glands of the skin of mammals may be mentioned as an example of special form, accommodating the regulation of temperature by facilitating loss of heat due to evaporation. Sebaceous glands, normally concerned with the lubrication of hairs, are modified as mammary glands for the secretion of milk.

The pharynx in vertebrates has become variously modified. Thus in fish it is the region perforated by the gill-slits. In the Tetrapoda it has become adapted to respiration on land, assuming the form already described in Chapters 7 and 8, the Eustachian tube alone remaining as a vestige of a gill-slit.

Body-coverings are typically scaly in fish, and their structure has already been described page 83). The scales of some reptiles – e.g., snakes – are purely epidermal structures. In birds and mammals the covering is of feathers and hair respectively, both primarily developed in connexion with the conservation of body-heat.

COLORATION IN ANIMALS. Perhaps the most striking instances of adaptation amongst animals are provided by a study of the various forms of coloration. These are approximately divisible into two classes. Protection is effected either through concealment, in which case the colours are sombre and blend with the environment, or else through the development of brilliant coloration, warning potential enemies of power to inflict harm upon them. In general, therefore, harmless animals adopt the former method of protection and noxious forms the latter. Stick- and leaf-insects afford striking examples of protective resemblance, since, in the resting state, both in coloration and in positions adopted, they are almost indistinguishable amongst the foliage. The caterpillar of the hawkmoth has a body green in colour, interrupted by black lines, whereby it is rendered inconspicuous. The black and yellow bands on the abdomens of hornets, wasps and bees provide examples of aggressive coloration.

But here a new phenomenon is encountered. If noxious insects acquire protection through the development of warning colours, the same protection may be afforded to species which, though actually harmless, display a similar coloration. This occurs quite commonly and is known as **mimicry**. Clear-wing moths and drone-flies superficially resemble wasps and bees respectively. One instance of mimicry in butterflies may profitably be considered rather more fully, since the genetic relationships

of the mimetic forms have been worked out in detail. It concerns a species of Indian swallow-tail, *Papilio polytes*. The male exists in one form only, but the female is trimorphic, two of the forms being mimetic of members of a different genus, alleged to be distasteful, whilst the third resembles the male. There are two factors (genes) concerned in the development of the various colorations, and they are borne on autosomes (page 580). Even so they exert no effect in the male: presumably the peculiar internal environment provided by the female is responsible for their becoming active. Such factors are said to be sex-limited in their effects. The *cyrus* form resembles the male. The presence of a factor, *A*, converts this into the *polytes* form, whilst another factor, *B*, in the presence of *A*, results in the production of the *romulus* form. Factor *B* alone exerts no effect. Thus the genotypes of the three forms may be represented as follows, where *a* and *b* denote the absence of the genes *A* and *B*, or at least the presence of allelomorphs which exert no observable effect on coloration.

Cyrus form	*Polytes* form	*Romulus* form
aabb	*Aabb*	*AaBb*
aaBb	*AAbb*	*AABb*
aaBB		*AaBB*
		AABB

The fact that the range of the mimic coincides with that of its model constitutes one of the strongest pieces of evidence in support of Natural Selection.

EMBRYONIC ADAPTATIONS. Adaptations are to be observed not only in adult organisms but also in various stages of their development. Thus in mammals a placenta is developed for the nourishing of the foetus during retention within the uterus. This structure is homologous with the allantois of lower forms, where its function is purely excretory. Various stages in the complicated life-histories of parasitic forms are to be regarded as adaptations to facilitate distribution, as already seen in Chapters 1 and 3. The absence of a larval stage in the life-history of the earthworm may be regarded as an adaptation to development on land.

ADAPTATIONS IN PLANTS. The majority of the structures now to be mentioned have previously been described, so that it remains to point out their adaptational significance.

Roots of higher plants are typically tap or fibrous. It has already been noted (page 289) that the leaves are adapted to the distribution of rain-water to the absorbent regions, directing it inwards to tap roots and outwards to fibrous roots. Similarly roots themselves vary according to the habitat of the plant which bears them, the fine ramifications of fibrous roots often penetrating great distances into arid soil, whilst tap roots are more characteristic of damp situations.

Leaves and stems are variously adapted to conditions of light-supply. Leaves are typically diaphototropic (page 457), whilst those growing in

shady situations are normally broad and thin and contain more chloroplasts. The cuticle is comparatively thin. The reverse of these conditions is exhibited by leaves growing in intense illumination. As already seen, leaves or stems of a plant may be modified to form spines, serving for protection. Where leaves are so constructed phyllodes (page 253) are common, whilst stems may become expanded to increase the photosynthetic area, as in the butcher's broom. Such expanded stems are known as **cladodes**.

Adaptations of plants to water-supply is a very important phenomenon, but it will be reserved for Chapter 38, where the relationship of organism to environment is discussed.

Adaptations to pollination and dispersal of seeds and fruits have already been considered (Chapter 16). It should now be clearly realised that in every case mentioned the adaptation is represented as a special form of a general structure – e.g., in a drupe the general structure is the wall of the ovary – the pericarp – which has here become divisible into three layers, as detailed on page 282.

Having regard to the definition of adaptation as the condition of harmony between organism and environment, it becomes at once apparent that this is not merely a desirable result of the operation of natural selection (of gene-complexes), but is the inevitable consequence. Organisms survive in the struggle for existence simply because they are properly adapted to their environment. Nor does this mean vague adaptation in the general sense. So severe is the struggle that refined degrees of adaptation may be sufficient to decide between survival and extinction: adaptation assumes very precise proportions. In terms of the selection of the gene-complex this would be expected. It is unlikely that the effects of a gene, even of an unestablished mutant gene, will be changed in different gene-complexes other than in the degree of their expression; in other words, their function will vary quantitatively from one complex to another. But assuming that natural selection is sufficiently severe, even these fine shades of variation in expression may decide the fate of contemporary gene-complexes. In this way those gene-complexes survive in which the 'best' genes have attained a position of dominance. It may, in fact, be said that the diagnostic features of any animal stock are the results of the expression of its dominant genes, operating as they do in highly favourable gene-complexes.

Conclusion

To all intents and purposes the currently accepted explanation of evolution is Darwin's natural selection hypothesis in modern dress. His original concepts stand. Variation in animal and plant form must occur and such variations must be heritable. There exists in nature a perpetual struggle for existence, in consequence of which the variations occurring are subjected to a continuous process of natural selection. It is now

appreciated that it is the gene-complexes of members of any given stock which are, in fact, selected. According to Darwin this selection results in the survival of the fittest. Today it is understood that selection is responsible for the assumption of dominance by all those genes most favourable to the stock's well-being. In other words the general picture has remained unchanged for a hundred years. We have, however, learnt to interpret the process of change implied by evolution in terms of the very bodies – the genes – responsible for the transmission, in stable form of detailed characteristics from parent to progeny.

CHAPTER 37

Classification

The theory of organic evolution obviously implies that relationship exists between various groups of animals and plants. That such is so is at once apparent.

Classification obviously involves progressive subdivision of groups, the differences between the members of which are becoming continuously smaller. Thus animals may be divided into Protozoa (non-cellular) and Metazoa (cellular), whilst each of these groups is then further subdivided. The Metazoa are arranged in phyla in such a way that as nearly as possible all the phyla differ amongst themselves to the same extent. The same consideration applies to further subdivisions, of which classes, orders, genera and species are the chief. Such subdivisions must necessarily be arbitrary, but the modern scheme of classification has achieved a remarkable degree of uniformity.

The general working of the classificationary scheme may best be understood by the selection of a definite example, and for this purpose we will consider ourselves faced with the necessity of indicating the diagnostic features of the Vertebrata, when we may proceed as follows.

The Vertebrata constitute a subdivision of the phylum Chordata, whose characteristics must therefore be described first. Both the Chordata and the higher Invertebrata (a collective term for the Metazoan non-Chordata, but of little classificationary value) have the following characteristics in common –

(i) They are bilaterally symmetrical, though in the Echinoderma the symmetry is often radial.

(ii) They are coelomate, though this is suppressed in the Arthropoda.

(iii) They are metamerically segmented, except the Mollusca. But the Chordata may be distinguished from the higher invertebrates by the following structural features occuring only in the former –

(i) An elastic, dorsal, skeletal rod – the notochord.

(ii) A dorsal, tubular nerve-cord.

(iii) A pharynx perforated by gill-slits.

(iv) A ventral heart through which blood flows in a forward direction.

As indicated on pages 627–28, the phylum Chordata is further subdivided into three subphyla, as follows –

SUBPHYLUM CEPHALOCHORDATA – e.g. *Branchiostoma*. Members of this group largely retain the primitive features associated with the

phylum Chordata, though a few specialised characters are superimposed – e.g. the extreme forward extension of the notochord and the multiplication of the gill-slits.

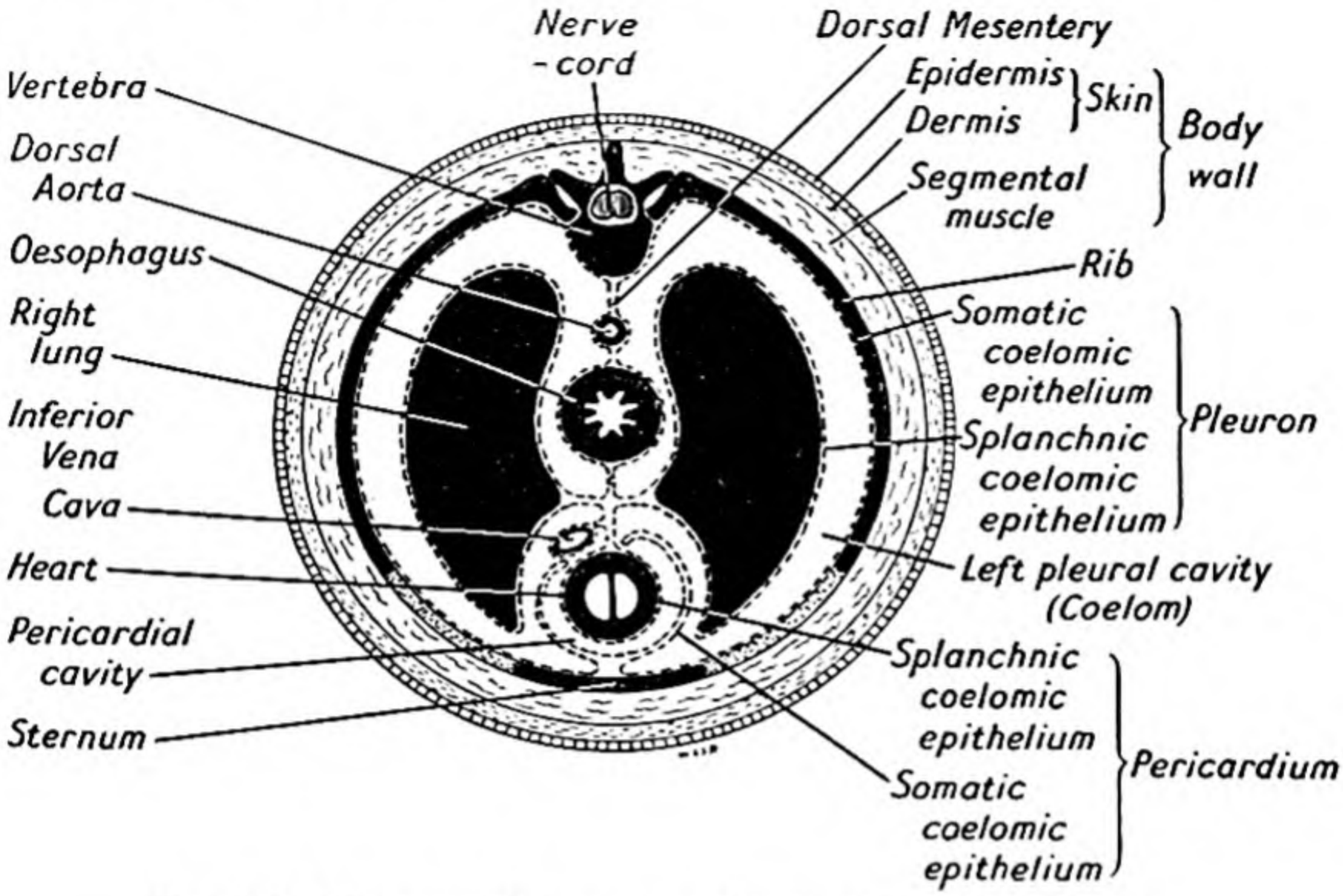


FIG. 339 – Diagrammatic Transverse Section through the body of a mammal in the region of the thorax.

SUBPHYLUM UROCHORDATA. These organisms show typical chordate characters only in the free-swimming larva, which is converted by a process of retrogressive metamorphosis into a sessile, degenerate adult.

SUBPHYLUM CRANIATA (VERTEBRATA). In addition to the general characteristics of the Chordata, members of this subphylum show certain diagnostic features of their own. Thus they possess –

(i) An internal skeleton of cartilage or bone.
(ii) A specialised head region, characterised by the presence of a brain enclosed within a skull.
(iii) Two sets of paired appendages, each member arising from several segments.
(iv) A tail supported by vertebrae and taking the form of a muscular appendage posterior to the anus.
(v) Separate dorsal and ventral nerve-roots.

The same progressive treatment is now extended to the various subdivisions of this important subphylum, indicated on page 627. Thus the Cyclostomata, characterised by the absence of jaws and exemplified by the lamprey, are separated from the jawed Gnathostomata, the charac-

teristics of whose five important classes are also stated on page 628 and which may be enlarged upon from knowledge gained of representative types in the early chapters of the book.

Of the various subdivisions none can be based on scientific definition. Even of species no exact definition is possible, as indeed would be expected if it is believed that evolution is still taking place. In the classificationary scheme given below, certain groups outside the scope of this book are mentioned, since they may quite possibly be encountered in practice by the student.

Classification of Plants

Plants are classified in a manner analogous to that adopted for animals, though the names given to the various divisions are somewhat different. A given plant is referred to by two Latin names, the first of which expresses its genus and the latter its species, as for animals. Thus the buttercup genus is *Ranunculus*, whilst in this genus there is included a number of distinct species – e.g., *bulbosus*, *repens*, *aquatilis*, *acris* and *arvensis*. Further subdivisions of species into varieties is often attempted, the differences being too insignificant and inconsistent to be regarded as a basis of specific distinctions. Genera are linked together into families, and particularly is this so in the Angiospermae, where such great diversity of structure is exhibited. Thus the family Ranunculaceae includes, for example, the genera *Ranunculus*, *Delphinium*, *Clematis*, *Anemone*, *Aquilegia* and *Caltha*. Following the scheme of plant classification on page 628, the principal features of a few families, in addition to those represented in Chapter 16 (i.e., Ranunculaceae and Leguminosae), will be stated. For the rest it will be assumed that the student is already aware of the characteristics of the various groups as a result of the study of individual representatives of them.

CLASSIFICATION OF ANIMALS

SUB-KINGDOM PROTOZOA – Non-cellular animals.

Phylum Protozoa

CLASS FLAGELLATA (Mastigophora), e.g., *Euglena* (page 642).

,, RHIZOPODA (Sarcodina), e.g., *Amoeba*.

,, CILIATA (Infusoria), e.g., *Paramecium*.

,, SPOROZOA, e.g., *Plasmodium*.

SUB-KINGDOM PARAZOA – Cellular animals, though cells retain a semi-independence.

Phylum Porifera (sponges).

SUB-KINGDOM METAZOA – Bodies consist of specialised cells.

GROUP DIPLOBLASTICA. Two layers to body-wall.

Phylum **Coelenterata**
CLASS HYDROZOA, e.g., *Hydra* and *Obelia*.
„ ANTHOZOA. Vertical partitions in enteron.
„ SCYPHOZOA. Hydroid phase largely suppressed.
GROUP TRIPLOBLASTICA. Three layers to body-wall.
Phylum **Platyhelminthes** – Flat worms.
CLASS TURBELLARIA. Free-living forms.
„ TREMATODA, e.g., *Fasciola*.
„ CESTODA, e.g., *Taenia*.
Phylum **Annelida**
CLASS POLYCHAETA. Chaetae borne on outgrowths of body, known as parapodia.
„ OLIGOCHAETA, e.g., *Lumbricus*.
„ HIRUDINEA, e.g., leeches. No chaetae: two suckers present.
Phylum **Rotifera**. Small animals: mostly fresh-water: possess ciliated trochal discs for locomotion, capture of food and respiratory purposes: posterior foot divided into two forceps: anterior part of gut a specialised chamber – the mastax – bearing teeth: frequently found in protozoan cultures.
Phylum **Arthropoda**. Jointed appendages: continuous exoskeleton.
CLASS MYRIAPODA, e.g., centipedes and millipedes.
„ INSECTA, e.g., *Periplaneta*.
„ CRUSTACEA, aquatic: two pairs of antennae; gills for respiration: e.g., the crayfish.
„ ARACHNIDA. Body divisible into two parts only – cephalothorax and abdomen: no antennae: four pairs of legs: e.g., the spider.
Phylum **Mollusca**. Body unsegmented: dorsal shell: ventral extension of body forms foot: respiration by thin dorsal extension of body-wall – mantle.
Phylum **Echinoderma**. Marine: radially symmetrical: mesodermal skeleton.
Phylum **Chordata** (see characters on page 626).
SUBPHYLUM CEPHALOCHORDATA, e.g., *Branchiostoma*.
SUBPHYLUM UROCHORDATA. Tunicates. Sessile organisms, showing chordate characters only in free-swimming larva.
SUBPHYLUM CRANIATA (Vertebrata).
Branch **Cyclostomata**. Absence of jaws – suctorial mouth: e.g., the lamprey.
„ **Gnathostomata**. Upper and lower jaws.
CLASS PISCES, e.g. *Scyliorhinus*. Cold-blooded with

covering of scales to the body; paired and median fins present, supported by dermal rays; persistent gill-clefts; no lungs, no embryonic membranes.

SUBCLASS CHONDRICHTHYES – skeleton composed entirely of cartilage.

SUBCLASS OSTEICHTHYES – skeleton contains bone; air-bladder present, but not used for respiration; no internal nares.

SUBCLASS DIPNOI – skeleton contains bone; air-bladder used as lung; internal nares present.

CLASS AMPHIBIA, e.g. *Rana*. Cold-blooded, with pentadactyl limbs; smooth skin; lungs; eggs without shells; no embryonic membranes; fish-like larva with gill-clefts, which are suppressed in the adult.

CLASS REPTILIA. Cold-blooded, with pentadactyl limbs; scaly skin; lungs; large, heavily-yolked eggs, with shells; embryonic membranes present; visceral clefts never bear gills.

CLASS AVES. Warm-blooded, with pentadactyl limbs, the anterior ones modified to support the wings; feathers; scales on legs; lungs; large, heavily-yolked eggs, with shells; embryonic membranes present; visceral clefts never bear gills.

CLASS MAMMALIA. Warm-blooded, with pentadactyl limbs; hair, but no scales; lungs; small eggs, devoid of yolk; gestation; young suckled; embryonic membranes present; visceral clefts never bear gills.

The classes Amphibia, Reptilia, Aves and Mammalia are grouped together for convenience as the **Tetrapoda**, characterised by the possession of pentadactyl limbs, whilst the three last-named classes, in which the embryos are contained within special foetal membranes, constitute the **Amniota**.

CLASSIFICATION OF PLANTS

I. **Thallophyta**. No distinct root and shoot system.

(A) ALGAE (see Chapters 9 and 10).

(i) Cyanophyceae (Blue-green Algae).

(ii) Chlorophyceae (Green Algae).

(iii) Xanthophyceae (Yellow-green Algae).

(iv) Phaeophyceae (Brown Algae).

(v) Rhodophyceae (Red Algae).

(B) BACTERIA (see Chapter 11).

(C) FUNGI (see Chapter 11).

(i) Phycomycetes (page 205, e.g., *Pythium* and *Mucor*).
(ii) Ascomycetes (page 205, e.g., *Penicillium*).
(iii) Basidiomycetes (page 209, e.g., *Agaricus*).
(iv) Lichenes (Algae and Fungi symbiotic together - see page 671).

II. **Archegoniatae.** Plants bearing archegonia.
(A) BRYOPHYTA. See Chapter 12.
(i) Hepaticae (Liverworts), e.g., *Pellia*.
(ii) Musci (Mosses), e.g., *Funaria*.
(B) PTERIDOPHYTA. Plants with definite roots and conducting system. Include ferns (Chapter 12) and *Selaginella* (page 556).

III. **Spermaphyta.**
(A) PTERIDOSPERMAE (page 590).
(B) GYMNOSPERMAE, e.g., *Pinus* (Chapter 13).
(C) ANGIOSPERMAE.
(i) Monocotyledons.
(ii) Dicotyledons.

In conclusion the main features of the more important families of Angiospermae will be considered. Those already done are the buttercup (page 270) and the sweet pea (page 271), representative of the Ranunculaceae and Leguminosae respectively.

I. Family **Cruciferae** – the wallflower (*Cheiranthus*).

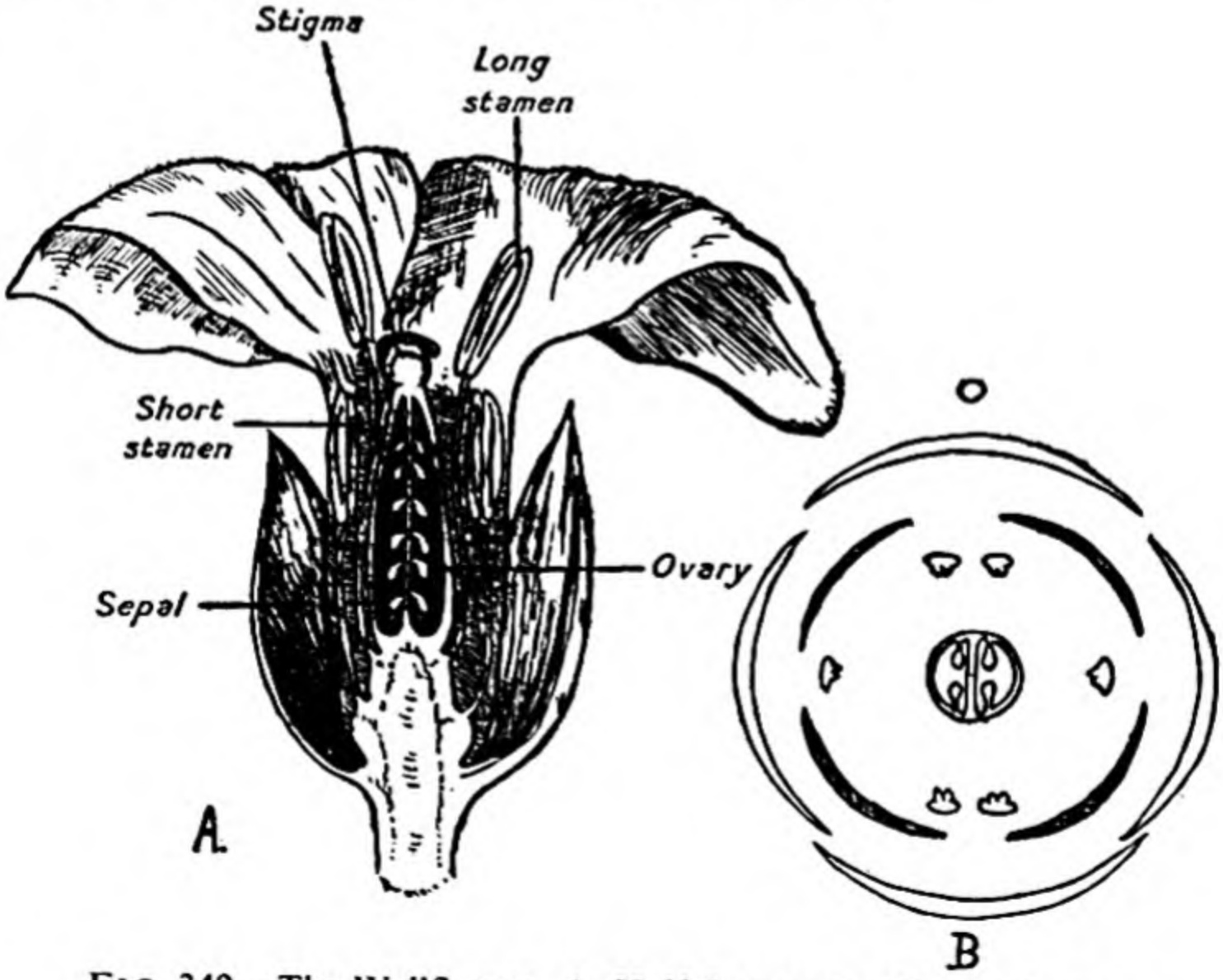


FIG. 340 – The Wallflower. *A.*, Half-flower; *B.*, Floral diagram.

INFLORESCENCE. Raceme.
FLOWERS. Actinomorphic, hermaphrodite and hypogynous.
CALYX. Four, free.
COROLLA. Four, alternating with sepals: in shape of Maltese cross and hence the name of the family.
ANDROECIUM. Six. Two in outer whorl: two pairs in inner – one anterior and one posterior.
GYNAECIUM. Two, united.

A floral diagram is given on page 631.

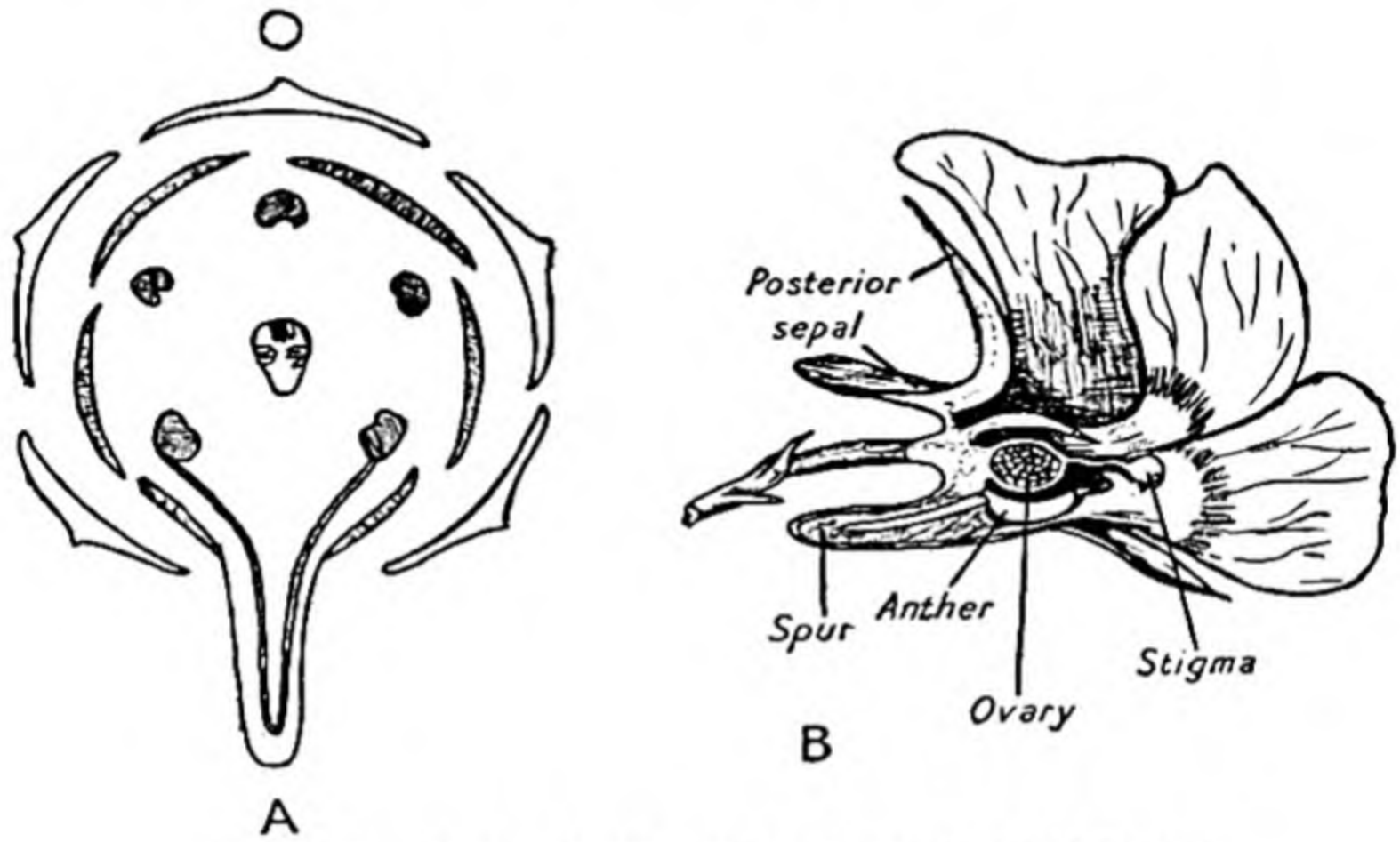


FIG. 341 – *Viola*. *A*., Floral diagram; *B*., Half-flower.

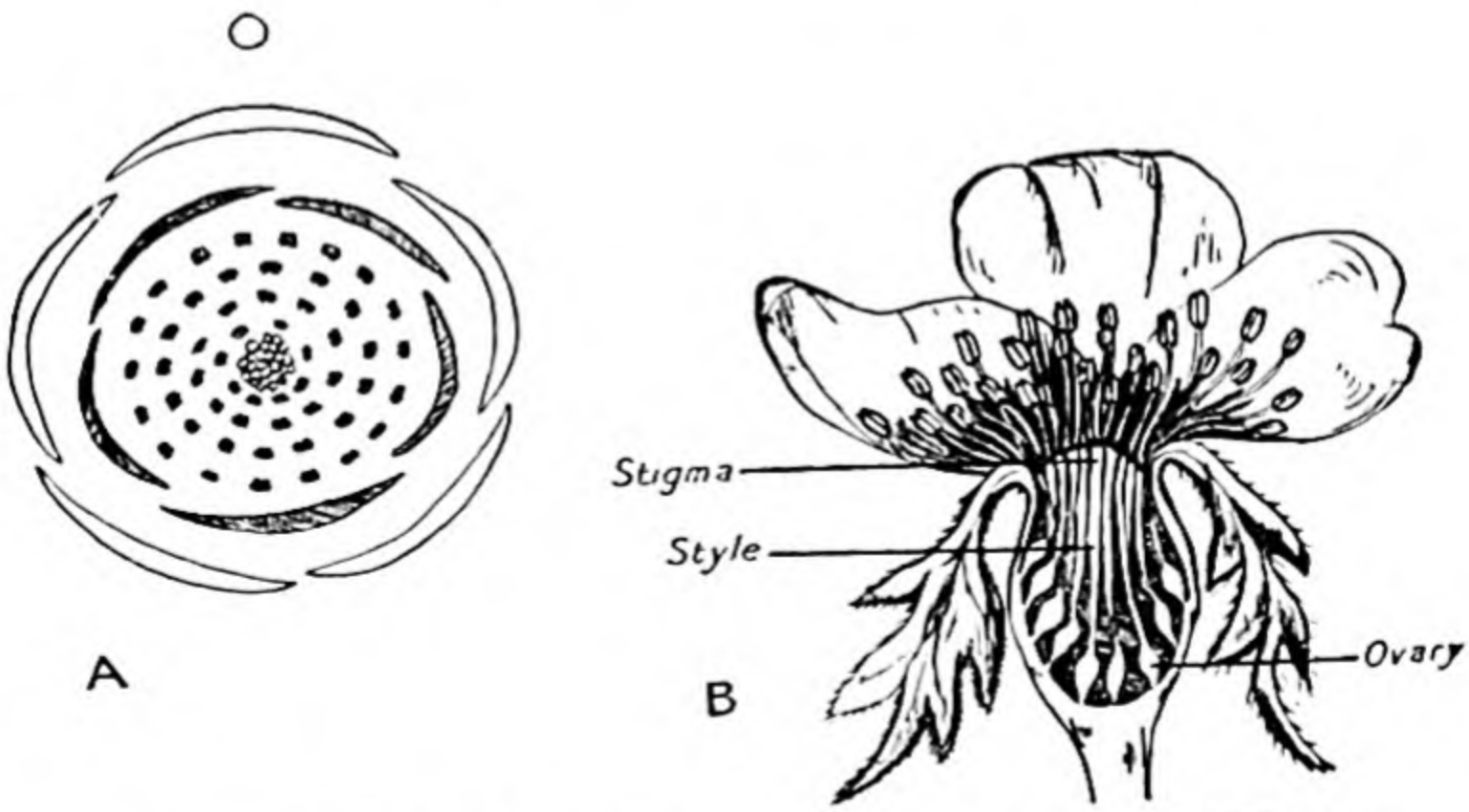


FIG. 342 – The Wild Rose. *A*., Floral diagram; *B*., Half-flower.

II. Family **Violaceae.** *Viola* is the only genus in Britain.
INFLORESCENCE. Usually solitary.
FLOWER. Zygomorphic, hermaphrodite and hypogynous.

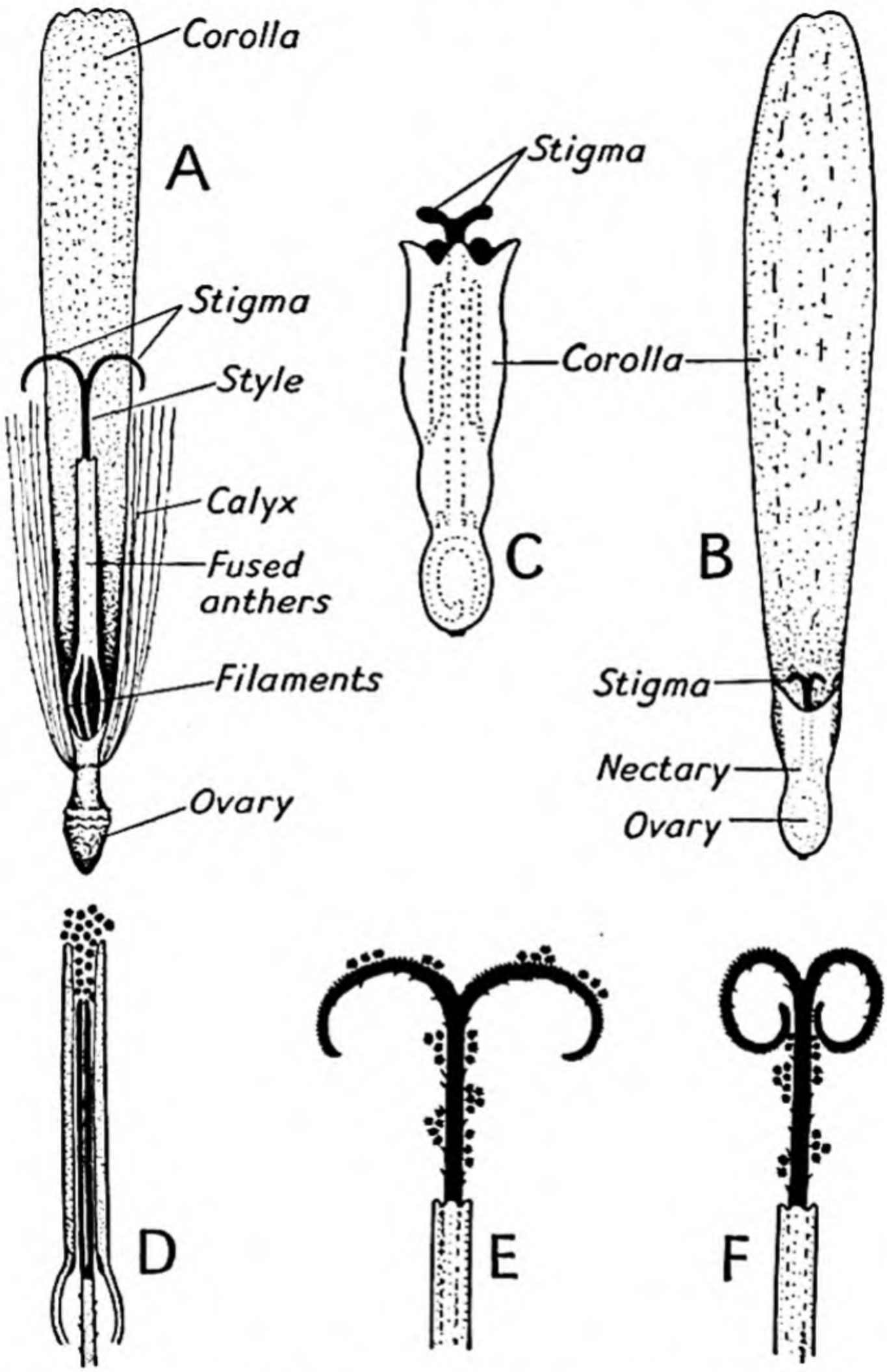


FIG. 343 – Florets of the Compositae. *A.*, Dandelion floret; *B.*, Ray floret of Daisy; *C.*, Disc floret of Daisy; *D.*, *E.*, *F.*, Stages in self-pollination by a Dandelion floret (for description see page 279).

CALYX. Five, free: each sepal projects backwards beyond its attachment to the receptacle.

COROLLA. Five, free: anterior petal bears a spur.

ANDROECIUM. Five, free: filament very short. Connective is continued beyond the anther, ending in an orange-coloured tip. Nectaries attached to two anterior stamens.

GYNAECIUM. Three, united.

III. Family **Rosaceae**. The wild rose will be taken as an example, though there is considerable diversity of form amongst the members of this family.

FLOWER. Actinomorphic, hermaphrodite and mostly perigynous, though epigynous forms occur – e.g. the apple.

CALYX. Five, free, with the odd sepal posterior.

COROLLA. Five, free.

ANDROECIUM. Numerous.

GYNAECIUM. Numerous carpels, free.

IV. Family **Compositae**, e.g., the dandelion and daisy.

INFLORESCENCE. Capitulum, surrounded by an involucre. All the flowers (florets) may be of the same type, as in the dandelion, or of two sorts, as in the daisy, namely:

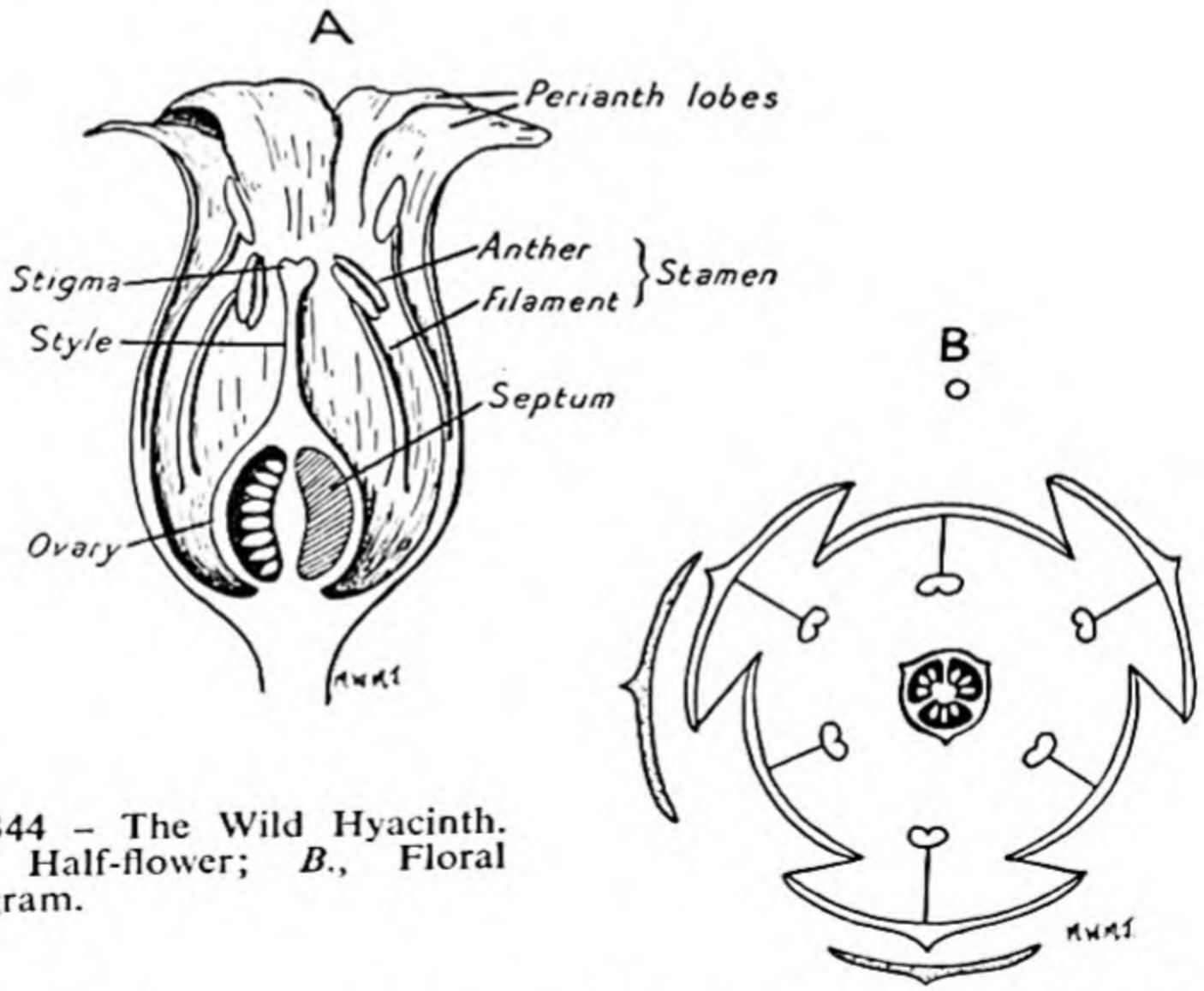


FIG 344 – The Wild Hyacinth. *A.*, Half-flower; *B.*, Floral diagram.

(i) **Ray florets** round the margin of the inflorescence. These are usually ligulate (strap-shaped) and pistillate (without stamens).

(ii) **Disc florets** in the centre. They are usually tubular and hermaphrodite.

FLOWERS. Zygomorphic, though disc florets may be actinomorphic: hermaphrodite or pistillate: epigynous.
CALYX. Absent or hair-like (dandelion).
COROLLA. Five, united; ligulate or tubular (see page 632).
ANDROECIUM. Five, epipetalous, syngenesious.[1]
GYNAECIUM. Two, united.

V. Family **Primulaceae**, e.g., the primrose.
INFLORESCENCE. Umbel very common.
FLOWERS. Actinomorphic, hermaphrodite and hypogynous.
CALYX. Five, united.
COROLLA. Five, united.
ANDROECIUM. Five, opposite the petals; epipetalous.

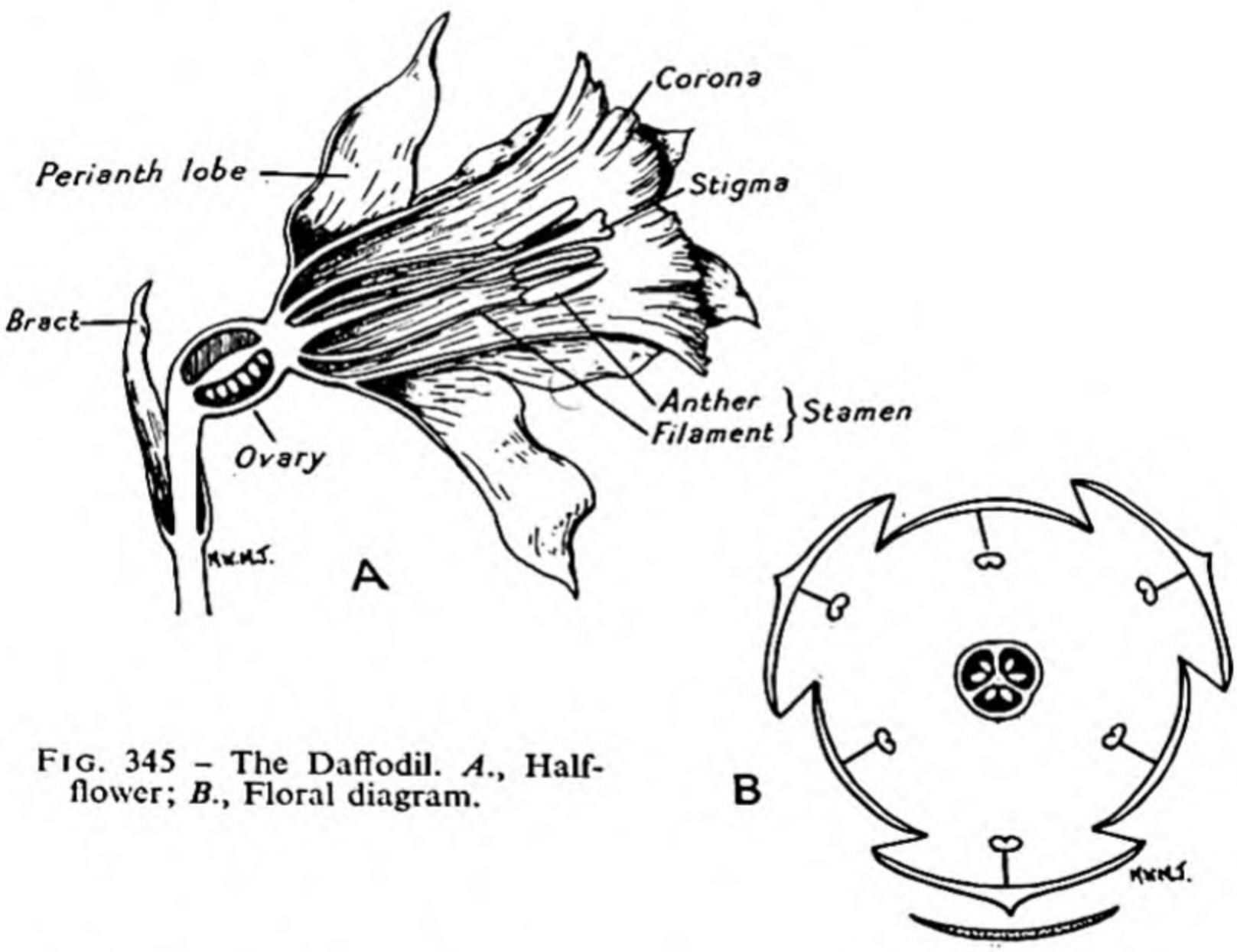


FIG. 345 – The Daffodil. *A.*, Half-flower; *B.*, Floral diagram.

GYNAECIUM. Five, united.
Note pin-eyed and thrum-eyed forms, as mentioned on page 279 and shown in section in Fig. 194, page 278.

VI. Family **Liliaceae**, e.g., the tulip and wild hyacinth.
FLOWERS. Actinomorphic, hermaphrodite and hypogynous.

[1] i.e., filaments free and anthers connected.

PERIANTH. Petals and sepals fused to form six petaloid perianth lobes: free (tulip) or united (wild hyacinth).
ANDROECIUM. Six, free (tulip) or epipetalous (wild hyacinth).
GYNAECIUM. Three, united.

VII. Family **Amaryllidaceae**, e.g., the daffodil and the snowdrop.
FLOWERS. Actinomorphic. hermaphrodite and epigynous.
PERIANTH. Six perianth lobes. In many members – e.g., the daffodil – an outgrowth forms a trumpet-shaped structure known as the *corona*.
ANDROECIUM. Six, free.
GYNAECIUM. Three, united.

As far as possible the families to which well-known and easily obtained flowers belong have been described. They serve to show the types of difference between one family and another. Text-books of botany should be consulted where knowledge of other families is required, though for present purposes a study of the families described above should provide a sufficient insight into the great variety of floral structure.

PRACTICAL WORK

In connexion with this chapter the student should learn to use a flora. Study very carefully the instructions for the use of the flora, and then practise on a few known flowers to see that the correct results are being obtained from observation of the characteristics of the flower and its application in the employment of the flora. Identify a number of unknown flowers, as may be pleasantly and profitably done on long rambles during the summer months. It is advisable on such excursions always to carry a hand-lens for the magnification of the smaller wild flowers.

PART VII

The Organism and its Environment

Up to now the various attributes of living organisms, both structural and physiological, have been described with but very little reference to purpose. Something of this was seen in Part VI, where the related problems of survival and adaptation were briefly discussed. The criterion of successful existence is adaptation to environment, facilitating survival both of the individual and of the race. In this concluding section something of the relationship between the living organism and the environment to which it responds, and by which its life-processes are so largely regulated, will be studied. An organism must be considered both in relation to other animals and plants, with which it may be associated in varying degrees, and also in connexion with the effects exerted upon it by purely inorganic influences, such as supply of water or range of temperature. Accordingly the two chapters in this section will concern themselves with the living organism in relation to its animate and inanimate environment. It is hoped that by the time this is completed a composite conception of the world of living things may be formulated, and that the connexion between structure, function and adaptation to environment may be fully appreciated. It must always be borne in mind that the division of biology into morphology, physiology, genetics and various other branches is one merely of convenience for description. The correlation of these is vital to the full understanding of that so fascinating object of study and embodiment of so great variety of form and function – the living organism.

CHAPTER 38

The Inanimate Environment

The problem of the origin of life is still an unsolved mystery. Suggestions have been made, which, whilst they may approximate closely to the truth, must necessarily remain hypothetical, unless or until they can be substantiated by experiment, which can take no form other than the creation of life in the laboratory. Even if this were achieved it might not even then explain the spontaneous origin of life. But the physico-chemical relationships between various grades of living organisms of to-day and their environment bring out one very significant fact. There is obviously a gradient between the physico-chemical constitution of the environment and that of the living organism, the difference between the two becoming progressively greater the higher the organism. Thus *Amoeba*, for example, consists merely of a small mass of protoplasm, appearing more or less homogenous throughout, except for its nucleus, though undoubtedly the compounds which comprise it are considerably complex. But in a mammal, for example, the variety of physico-chemical composition is infinitely greater, and therefore more completely different from that of the environment. Further, the gradient between organisms and environment in respect of such physical characters as temperature, density and concentration of salts is at its steepest in the highest animals, whilst in *Amoeba*, for example, and especially in marine and parasitic Protozoa there is practical identity of these factors within and without the organism. It may be possible to trace this gradient backwards until eventually it would lead to the origin of life, where presumably the earliest organisms showed considerable resemblance in composition to the environment which supported them. Such a conception is merely an extension of the theory of evolution, this time of living from non-living matter. It can only be postulated that conditions at the time of the origin of life were favourable to the aggregation of molecules of then-existing substances into bodies of such form and dimensions as to display in a very elementary way the manifestations characteristic of life. They grew in size by the assimilation of substances closely akin in nature to their own bodies, and one of the principal signs of progress in the evolution of living organisms may well have been the ability to support themselves on materials progressively less like their own body-substance. At a comparatively early stage this may have resulted in a fundamental division of living organisms into two types. One of these possessed a pigment, similar to, or perhaps identical with, chlorophyll, whilst the other

elaborated a mechanism for the chemical solution of foods, which, though still complex, were to varying degrees dissimilar from their own protoplasm. Upon these two important developments appear to depend the great majority of the differences between animals and plants as they now exist, so that it is opportune for these differences now to be considered.

Differences between Animals and Plants

In principle the following considerations will apply to higher animals and plants, since they represent the results of the progressive divergence of the two groups during the process of organic evolution. Reference to exceptions to the general rules will be made, whilst in conclusion an organism demonstrating some of the characteristics of both will be considered.

NUTRITION. This will be dealt with first, since, as pointed out above, most other differences may be regarded as dependent upon it. The food of animals consists of complex organic substances, which are taken into the body in solid form. They are rendered soluble by digestion, after which they are absorbed, distributed and converted into body-substance. The process is essentially one of decomposition, followed by synthesis. Plants absorb simple foods in aqueous solution or in the gaseous state. The water and carbon dioxide are combined to form sugars in the process of photosynthesis, whilst mineral salts are subsequently incorporated in the production of proteins. The whole of their nutrition is essentially synthetic. Plants without chlorophyll behave in a manner closely resembling that of animals, for they absorb complex foods, though in liquid form. The insectivorous plants and many Fungi resemble animals even more closely, since their food is, in the first instance, solid.

MOTILITY. The motility of animals was doubtless developed in connexion with the search for food. There are very few but what possess this power. Some Coelenterata afford exceptions. Thus a coral lives an attached mode of life, food being captured and conveyed to the mouth by the distensible tentacles. Plants are characteristically sessile. They are completely surrounded by their food, the roots by a dilute solution of mineral salts and the shoot by an adequate supply of carbon dioxide. Only a few of the non-cellular Algae exhibit powers of locomotion. Many of these reproduce rapidly, so that the ability to move may well accommodate distribution.

EXTERNAL FORM. It is manifestly an advantage to animals that, being motile, their bodies should be compact. But with plants the reverse is the case. Both root and shoot expose a large surface for the absorption of food. Thus both become arborescent, whilst the shoot is further characterised by the formation of leaves as flattened expansions for the presentation of a considerable surface-area to facilitate rapid photosynthesis.

The relative position of supporting tissues of the body in animals and

plants is interesting. Most importantly – in the vertebrates – the skeleton takes the form of axial rods, supporting the trunk and limbs. Being jointed these rods do not impair flexibility. Where exo-skeletons occur, as they do so commonly, they usually consist of plates jointed in such a way that locomotion is not impeded. This is evident from a study of the exo-skeleton of the cockroach. In plants the strengthening tissue is more nearly peripheral, and always unjointed. Thus in unthickened stems it is usual to find in the outer layers of the cortex considerable quantities of collenchyma and sclerenchyma, whilst in the thickened stem the bark serves an important supporting function. It is true that the whole of the secondary xylem is most important in this respect in many trees, but many plants, including some trees, possess stems which remain hollow throughout life. This peripheral support is obviously in adaptation to sessility, since rigidity is the prime necessity of any such skeletal structure.

RESPONSE TO STIMULI. Plants respond primarily to such stimuli as affect their direction of growth, and their responses are collectively termed tropisms (Chapter 26). These are of importance in that they normally result in the upward growth of the shoot to the region where maximum sunlight is available, whilst the root quickly penetrates for a considerable distance into the soil, affording firm anchorage and reaching the position where water is most plentiful. The hormonic explanation of these movements represents an important advance in biological discovery. Since the environment in plants is comparatively uniform the latter have no need to exhibit response to anything like the wide variety of stimuli which regulate the behaviour of animals. So great is the number and so important the response elicited that the conduction of impulses in animals is effected through specialised nervous tissue, whilst sense organs are developed for the perception of the stimuli of sight, hearing, taste and smell. Further, the response may be effected by muscles some distance away from the region of perception, so that conduction of impulses must needs be effected. Such conduction as occurs in plants has already been described (page 489). Occasionally amongst the Algae forms are found to be light-sensitive, owing to the possession of a stigma. In such forms the movement occasioned normally results in their reaching the optimum light-intensity for photosynthesis, whilst in animals irritability is largely of nutritional significance.

RESPIRATION. Owing to their powers of locomotion animals are great consumers of energy. Accordingly the respiratory mechanism is highly developed, ensuring frequent and rapid gaseous exchange at some richly-vascularised surface. The oxygen is subsequently distributed to the tissues in the blood. In the Insecta it is carried direct to the tissues through the tracheae (page 75). In plants the distribution of oxygen can be accommodated sufficiently rapidly merely by diffusion through intercellular spaces from stomata and lenticels. In general it may be said that animals are the great consumers of energy, decomposing organic sub-

stances with the liberation of mechanical and heat energy, whilst plants synthesise their protoplasm from inorganic substances and are the great storehouses of energy. The ability to respire anaerobically is regarded as a primitive property of all plants, though developed to a much greater extent in some than in others. In animals its occurrence is confined to a few internal parasites.

ELIMINATION OF WASTE. In accordance with their greater expenditure of energy it is only to be expected that in animals a greater proportion of waste substances, both liquid and gaseous, will be produced. Thus a frequent and regular elimination of these substances is practised. Further, the food of an animal is solid, whilst some part of it resists the action of digestive juices. This too must be eliminated regularly. In plants waste substances may frequently be withdrawn from circulation and employed secondarily to fulfil some non-metabolic purpose, as instanced in Chapter 25. Others are deposited in the leaves, for example, where they are eliminated at leaf-fall.

REPRODUCTION. Reproduction is essentially similar in animals and plants, though refinements have occurred the more completely to adapt each to its particular mode of life. In the lower forms it is effected by binary fission, whilst in all others sexual reproduction involves the fusion of two gametes, identical in some of the lower members of both groups, and in the higher completely differentiated into male and female. Certain differences are, however, apparent. The regular alternation of generations in plants and its absence from the life-history animals has already been noted, whilst a comparison between the egg of an animal and the seed of the Spermaphyta has already been drawn (page 561). The principal significance of the reproductory process in plants is the way in which pollination and distribution are effected, so necessary on account of the sessile character of plants.

It will be realised from the above consideration of the differences between animals and plants that no definition can be formulated which will completely separate them. This is only to be expected if the conception of their community of descent is accepted, for certain characteristics of each group may well be anticipated to occur exceptionally in members of the other, perhaps perpetuated from their common ancestors or perhaps arising anew. *Euglena* affords a very interesting example of an organism displaying certain characteristics of both animals and plants.

Euglena

Euglena viridis is normally classed as a Protozoön, but it is especially interesting on account of its possession of chlorophyll, so that it is frequently responsible for the green colour of the puddles in which it lives. It is a minute, spindle-shaped organism, blunted at its anterior end. It has a peripheral **ectoplasm**, covered with a thin **cuticle** and enclosing the granular **endoplasm**. At the anterior end is a depression, known as the

gullet, at the base of which is set a **flagellum**. This takes the form of a long, thin projection, consisting of an axial filament surrounded by contractile protoplasm. At its base it is in contact with a pair of basal

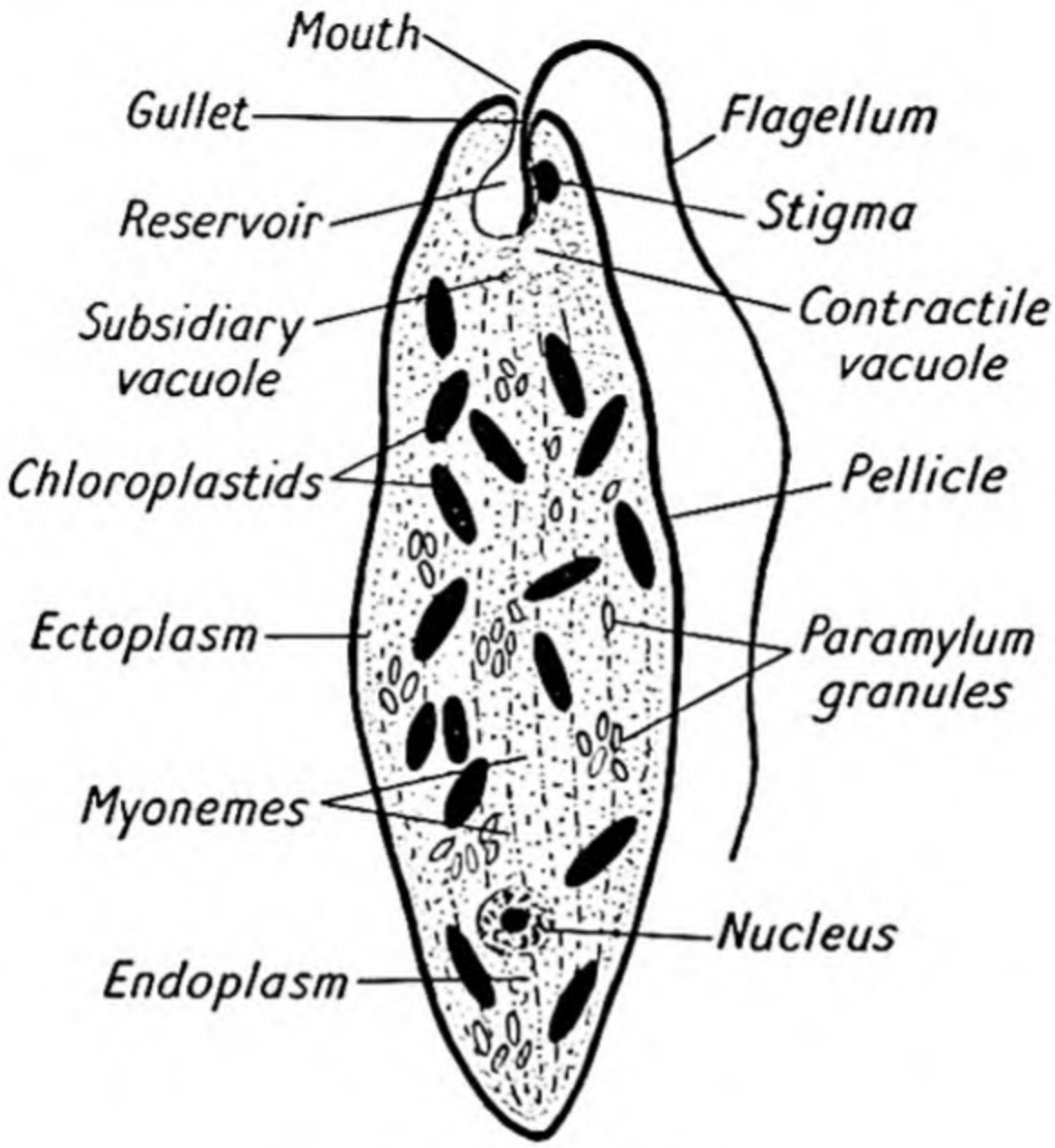


FIG. 346 – *Euglena viridis*.

granules, or **blepharoplasts**, related to its activity. Locomotion is effected by the backward beating of the flagellum, whilst the performance of wriggling movements by the organism demonstrates the general contractile properties of the ectoplasm. There is a central spherical **nucleus**, whilst many discoid **chloroplasts** also lie embedded within the endoplasm. There are numerous **pyrenoids** present (page 182), each of which is surrounded by a number of **paramylum** granules. Paramylum is a substance very like glycogen in chemical composition. Near the base of the gullet is a bright red, light-sensitive eye-spot, or **stigma**, consisting of droplets of an oily liquid, coloured red by haematochrome, surrounding a lens-like paramylum granule. *Euglena* is phototactic – i.e. it moves towards a source of light, providing it is of not too great intensity. At the base of the gullet is the vacuolar apparatus. This is of composite nature, consisting of a **contractile vacuole**, which is itself contributed to by a number of **accessory vacuoles** and which discharges its contents into a **reservoir**, communicating with the gullet.

Euglena is capable of holophytic nutrition, and in this respect it is essentially plant-like. The paramylum granules represent the direct products of photosynthesis, corresponding to the starch of green plants. But *Euglena* differs from green plants in that it is capable of assimilating dissolved organic matter, and if this is present in appreciable quantities the chloroplasts gradually disappear. Under ordinary conditions it probably combines both modes of nutrition, though the gullet does not serve for the taking in of food, as might be expected. The possession of a contractile vacuole is an animal, rather than a plant, characteristic. Whilst some waste matter may well be exuded from it, it probably serves in the main for the elimination of excess water, which has entered by osmosis. In its response to light it closely resembles many motile, non-cellular Algae – e.g., *Chlamydomonas*. *Euglena* is generally accepted as an animal in which certain plant attributes have been developed secondarily. Only by this conclusion can the presence of a gullet be accounted for, namely as a structure which formerly accommodated the entrance of food, probably solid, as, for example, in *Paramecium*. The most important deciding factor would appear to be the ability of *Euglena* to live holozoically, a characteristic unknown in green plants.

Reproduction is effected by longitudinal division, beginning at the anterior end. Previous to this process the organism not infrequently encloses itself within a gelatinous cyst, mucilage being secreted by the ectoplasm. Often the encysted products of division form further cysts and repeat the process of division. In this way a body, known as a **palmella**, may be formed, not unlike that of *Chlamydomonas*. No sexual phase has been confirmed in the life-history.

Unusual Environments

The general adaptation of living organisms to their environment is so universal that any exception to it is regarded as anomalous. Such adaptation may well be noticed by a consideration of the bodily form of various animals and plants living under abnormal conditions.

In animals cave-dwelling forms show considerable degeneracy of organs of locomotion and stimuli-perception. Thus they are usually blind or semi-blind, whilst almost all pigment disappears. An example is afforded by *Amblyopsis*, a blind cave fish. Burrowing forms have their appendages considerably modified. Thus the digits of both fore- and hind-feet are frequently directed backwards and assist in digging operations, whilst the eyes and ears are sunk into the thick fur. Aquatic mammals – e.g. the whale and the seal – have their limbs modified as paddles, whilst the limbs of pterodactyls and bats show adaptation to gliding and flight respectively. Deep-sea animals are variously modified. Thus many fish develop brilliant phosphorescent organs, mainly of sexual function but possibly serving to attract other organisms on which the animals prey. Others have long, delicate, sensitive structures by which

they find their way about in the darkness. Sponges show parallel modifications, for they are frequently of parachute shape, whereby they, like the flat-fish, are prevented from sinking into the ooze.

SOIL

A very important feature of the inanimate environment of rooted plants is the soil in which they grow. For purpose of description soil may best be analysed into four separate components, namely its mineral content, its organic content, its living content and its atmosphere.

MINERAL CONTENT. This has been formed as a result of the action of weathering of rocks, mainly by water containing dissolved carbon dioxide and by frost. Thus the nature of a particular soil depends first upon the type of rock from which it has been derived. Soils differ not only in the chemical nature of their mineral component, but also in the diameter of the particles. Based on this latter criterion soils may be classified into four groups –

Coarse sand – 0·2 to 2·0 mm.: *fine sand* – 0·02 to 0·2 mm.
Silt – 0·002 to 0·02 mm.: *clay* – less than 0·002 mm.

A rough mechanical analysis of soil may be made by placing a small quantity of soil into a tall gas-jar and then nearly filling with water. The whole is then stirred until a liquid of uniform turbidity is obtained, after which it is allowed to settle. (See Fig. 347.)

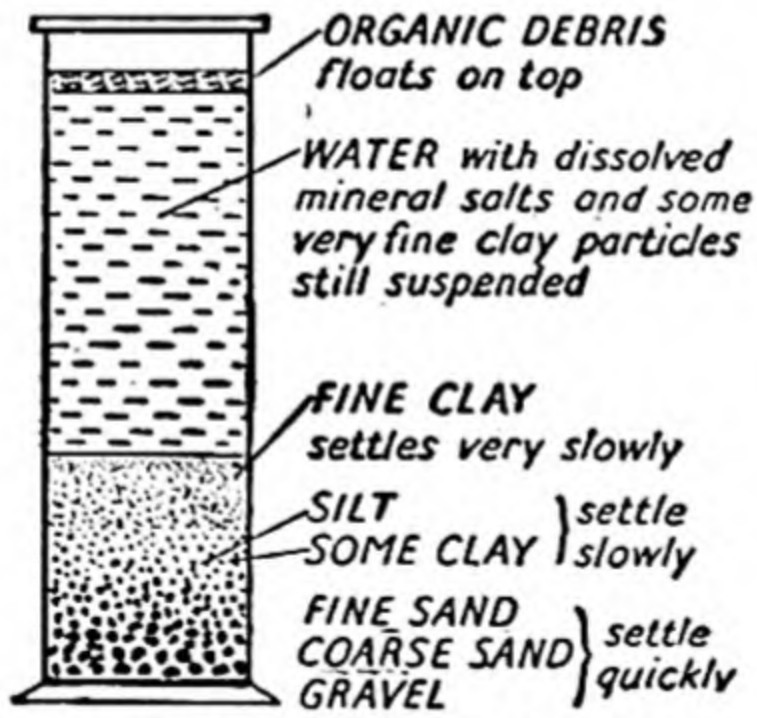


FIG. 347 – Diagram to show results of the mechanical analysis of soil.

The size of the particles has a very important bearing on the reaction of the various soils to water, determining their permeability and powers of retention. These phenomena can be investigated experimentally. The total water-content of soil is divisible into three categories – gravitational water, capillary water and hygroscopic water. An analysis of the

water-content of soil may be made by taking a known weight of soil (100 gms. for convenience) in an evaporating dish and heating it to constant weight over a water-bath at a temperature a little short of 100° C.

To compare the permeabilities of various soils to water the apparatus shown in Fig. 348 is employed. Take great care that the soil in all three

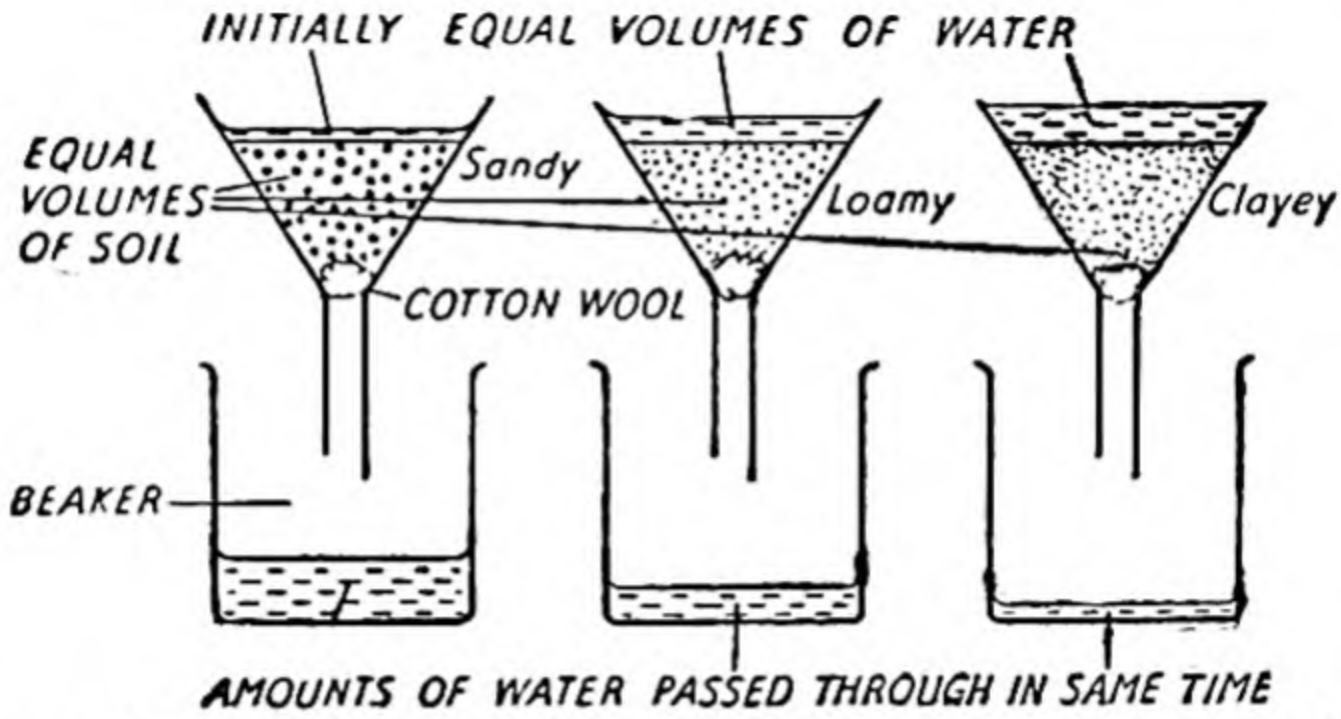


FIG. 348 – Diagram of apparatus for comparison of permeabilities of various soils to water.

funnels is equally wet and is packed to the same degree of tightness. By comparing the rates at which water collects in the beakers, after dripping has commenced in all three cases, relative measurements of the permeabilities of different types of soil may be made.

The same form of apparatus may be employed in the determination of the powers of retention of water by various types of dry soil. On this occasion the water passing through is collected in measuring cylinders and, when dripping has ceased, the amount collected is subtracted from the original volume, which this time must be known.

Gravitational water is that which will drain away from a soil under the influence of gravity, as in the above experiments. *Capillary* water is that which adheres by surface-tension to the surfaces of the soil particles. The smaller the particles in a given volume of soil the greater will be their total surface-area, and consequently the greater their power of retention of capillary water. This capillary water is of great importance to plants, for root-hairs in contact with it are able to absorb considerable quantities of it. But as the soil becomes drier these films of capillary water become thinner. Thus water, although present, becomes progressively less available to the plant, so tenaciously do these films adhere to the surfaces of the particles. It is not always realised that a soil covered with a surface-crust loses water *more* rapidly than does a loosened soil. This is because the matted soil provides numerous capillaries for the escape of water to the surface: it is further harmful in preventing free exchange of gases.

The rates at which water rises through various soils as a result of capillarity may be investigated by means of the apparatus shown in Fig. 349. The specimen soils are dried by long exposure to air and rubbing with the hands, and equal volumes are placed into each of the

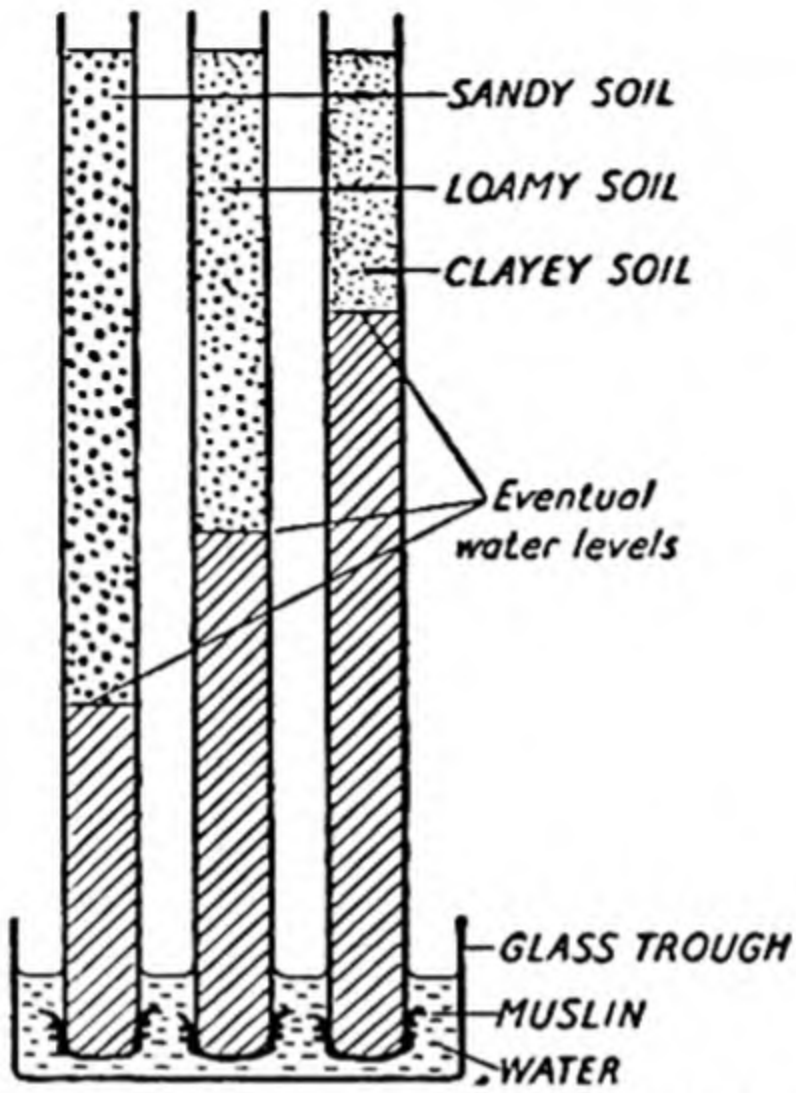


FIG. 349 – Diagram of apparatus for investigation of the rates at which water rises through various types of soil.

three wide glass tubes, which are open at both ends. The heights of the columns of water gives an indication of the relative capillary-powers of the specimens.

Finally, hygroscopic water is that imbibed by the soil colloids or present as water of crystallisation.

Reference has been made so far to soils found on their site of formation. But running water does much to transport soil particles from one place to another. Where and when they will again be deposited depends partly upon their own size and partly upon the rate of flow of the water. This accounts for the formation of gravel banks and large tracts of alluvial soil at the mouths of rivers. Furthermore, most natural soils are mixed, being composed of particles of differing sizes and chemical nature, though usually with one type predominating. Thus soils may be sandy gravels (e.g. a pebble beach), clays (e.g. London Basin), or silts (e.g. near river estuaries). Intermediate between these are *loams*, which contain sand and clay particles in approximately equal proportions. Very frequently loams are almost entirely devoid of calcium carbonate. Clay soils in which calcium carbonate (limestone) is present are called *marls*.

Soils which contain a high proportion of clay are cold, heavy and difficult to work. They may be lightened most easily by the addition of a top dressing of lime. The lime serves to decrease the cohesion between the particles of clay and a simple experiment may be performed to demonstrate this. A little clay is shaken up with water in a tube and left to stand. After some days it is observed that the water above the sediment is still cloudy, due to the presence of colloidal particles of clay. If a little 10% lime-water is now added there is a rapid clearance. Under the influence of lime, particles of clay are said to become *flocculated.*

In general, mineral salts are present in sufficient quantity in all soils to promote plant growth, though some, like common salt and calcium carbonate, exert a regulatory influence over the type of vegetation. For the most part it is the *physical*, rather than the chemical, nature of the soil which determines the vegetation. Climatic factors are themselves of direct importance.

ORGANIC CONTENT. This is composed of the dead remains of the former inhabitants of the soil, including those parts of plants which in life extend above the soil: it is termed the *humus*. It darkens the colour of the soil, and this makes it possible, if a cutting be examined, to distinguish between the soil and the *subsoil*. This latter is composed of rock particles in the process of conversion into true soil and is not normally penetrated by the roots of plants. The amount of humus can be determined by the heating to constant weight, in a crucible, soil which has previously been dried in the experiment to determine its water-content. There is, however, an appreciable source of error in this experiment, in that much of the hygroscopic water will not have been eliminated at 100° C., whilst at the temperature reached in the crucible metallic carbonates may decompose with the liberation of carbon dioxide. Humus normally occurs in a state of almost complete disintegration, due largely to the activities of earthworms. *Peat* is an exception to this. It consists of plant remains, laid down in conditions unfavourable to decomposition and is therefore to be found in deposits reaching considerable depths. It is upon this organic content of the soil that Bacteria – notably those concerned with the circulation of nitrogen – work. Thus the valuable content becomes available again to later generations, only to be replaced by perpetual decay. Humus may be added with advantage to garden soil, for not only is it of intrinsic value but it also does much to lighten a heavy soil.

LIVING CONTENT. Of paramount importance in the soil are Bacteria. These are responsible for the putrefaction of all organic matter which reaches the soil, and in particular those responsible for the transformation of nitrogenous compounds are of very great significance. Reference has already been made to these Bacteria on page 410 *et seq.*

The importance of earthworms in the aeration of soil, the disintegration of humus and the tillage of the soil have already been referred

to. The benefits from their activities are inestimable.

In addition the soil may harbour organisms having deleterious effects upon plant life. Thus the oöspores of *Pythium*, for example, may be there ready and waiting for appropriate conditions to germinate and cause 'damping off' of seedlings. The soil is also the home of many insect larvae, some of which may themselves do damage to plants or give rise to *imagines* which will do so. Thus the wireworm is the larva of the click-beetle, and the leather-jacket of the crane-fly. The cockchafer larva does great damage to the roots of grasses. The soil also contains resting stages of organisms parasitic upon animals. Such are exemplified by the eggs of the roundworm (*Ascaris lumbricoides*) and the spores of the Bacteria responsible for tetanus and anthrax. But organisms productive of adverse effects, more particularly in relation to plant life, are in a very small minority in the soil.

Soil Atmosphere. It is of the utmost importance to the roots of growing plants that they be plentifully supplied with air, the oxygen of which is essential for respiration, thereby providing the energy necessary for growth. Oxygen is also required to maintain the energy-supply of much of the animal and plant population of the soil. The soil atmosphere can only be maintained if the surface soil is loose, thus permitting free gaseous exchange to take place with the air above.

The amount of air in a given sample of soil may be determined by means of a simple experiment. Water is placed in a large gas-jar or beaker, into which is lowered, mouth upwards, a small tin can, until completely submerged. The level of water in the gas-jar is marked with a strip of gummed paper. The tin can is now very carefully drawn upwards and, when out of the water, is held while water clinging to the outside drips back into the gas-jar: the can itself is still full to the brim. Once dripping has ceased the can is completely withdrawn and emptied. A few holes are now carefully bored in the bottom of the can (great care must be taken not to alter its shape), which is then driven mouth downwards into the soil to be tested. It is then dug out and the contained soil cut off flush with the surface. The can is then returned to the gas-jar of water and, when completely submerged, the soil is scraped out. It will be found that the new level of water in the gas-jar falls short of the original, and the difference between the two represents the volume of air in the soil. It can be determined by adding water from a burette until the former level is reached and noting the amount required.

It is important to growing plants that the soil should be permeable not only to water but also to air. An experiment may be performed to demonstrate the relative permeabilities of various soils to air. The apparatus shown in Fig. 350 is employed. To the top of each of three burettes a filter-funnel is attached by means of rubber tubing, the burettes being first completely filled with water. A small plug of cotton wool is then placed in each funnel, and then each is filled, equally compactly,

with a sample of soil – e.g. sand, loam and clay respectively. The taps of the burettes are then opened and the amount of water leaving each burette in a given time affords a measure of the permeability of each type of soil to air.

Thus the properties of soil in relation to plant life depend upon the

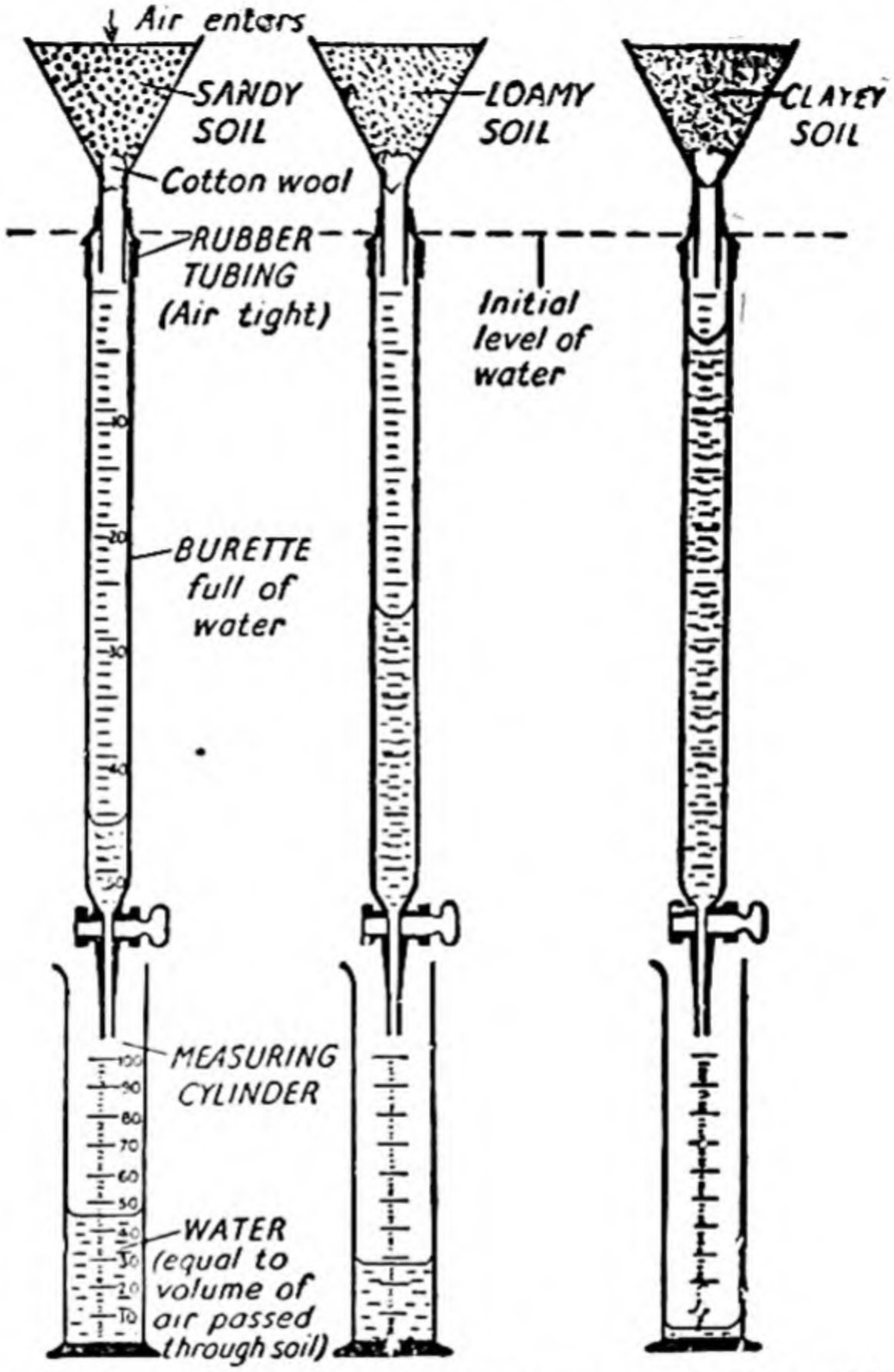


FIG. 350 – Diagram of apparatus for comparison of permeabilities of various soils to air.

physical and chemical nature of the particles, though predominantly upon the physical, for these regulate the supply of two supremely important requirements for successful growth, namely water and air.

Plants and their water-supply

In Chapters 14 and 15 the stem and leaf of a plant growing under

average conditions were described. It is now necessary to inquire to what extent and along what lines this becomes modified in hydrophytes (aquatic plants) and xerophytes (plants growing in arid soil).

(A) HYDROPHYTES. Hydrophytes frequently exhibit various characteristics of etiolation (page 421), as would be to some extent anticipated, since they grow in conditions where the supply of light may be materially reduced. Thus the internodes are usually elongated. In Fig. 351 is seen a transverse section of a stem of the mare's-tail (*Hippuris*). A great development of air-spaces in the cortex has occurred. These serve partly to render

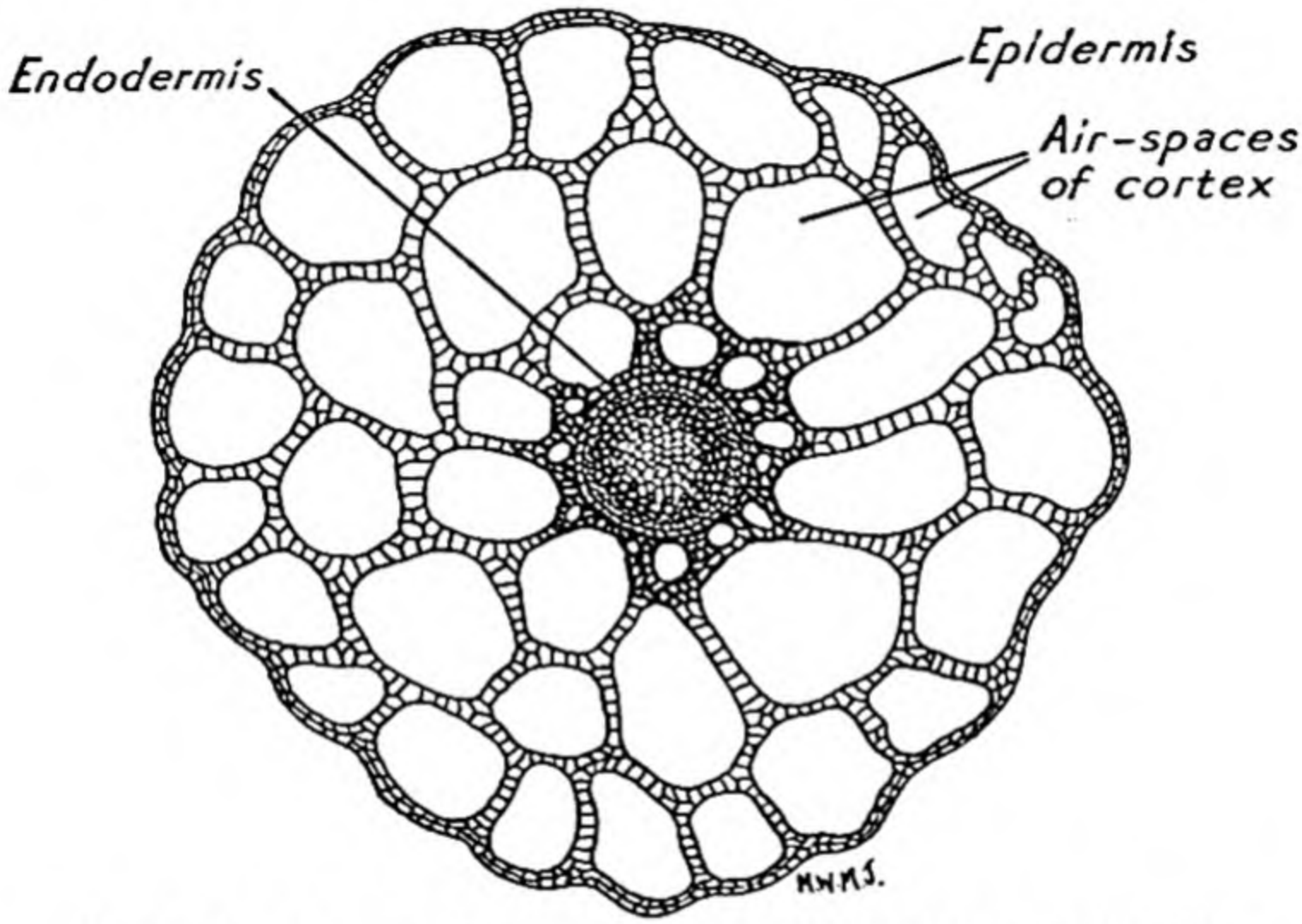


FIG. 351 – *Hippuris*. Transverse section of the stem. Note the great development of spaces and the reduction of the vascular elements.

the stem lighter and partly to facilitate a greater distribution of dissolved oxygen for respiratory purposes. The stele assumes the form of a thin, axial rod, thereby enabling the plant to bend more easily with the movements of the water. Since absorption of water and salts is not confined to a root, the xylem and phloem are considerably reduced in extent and differentiation. The leaves of aquatic plants are frequently very finely divided, thereby increasing as far as possible the assimilating surface, as well as cutting down their resistance to water currents. The central portion encloses considerable air-space, whilst the vascular elements are very much reduced. Submerged leaves rarely contain stomata, whilst in floating leaves these structures occur on the upper surface. Since this latter is normally covered with a delicate, wax-like secretion it is not readily wetted, so that the stomatal pores are thus protected from closure by a

film of water. Aërial leaves of water plants show considerably less modification from those found in mesophytes. In plants only partly submerged transpiration still proceeds through the stomata of the aërial leaves. A transpiration stream persists even in submerged plants, which often possess hydathodes (page 381).

(B) XEROPHYTES. Xerophytes are plants living in conditions of shortage of available water. Certain structural features associated with them are described as xeromorphic characters, sometimes assumed by plants which are not true xerophytes (see page 261). According to the means adopted for the withstanding of drought, xerophytes are divided into three classes, each of which will be briefly considered individually.

(*a*) *Drought Endurers*. An examination of the leaves of various xerophytes of the non-succulent type show that the surface is protected by a

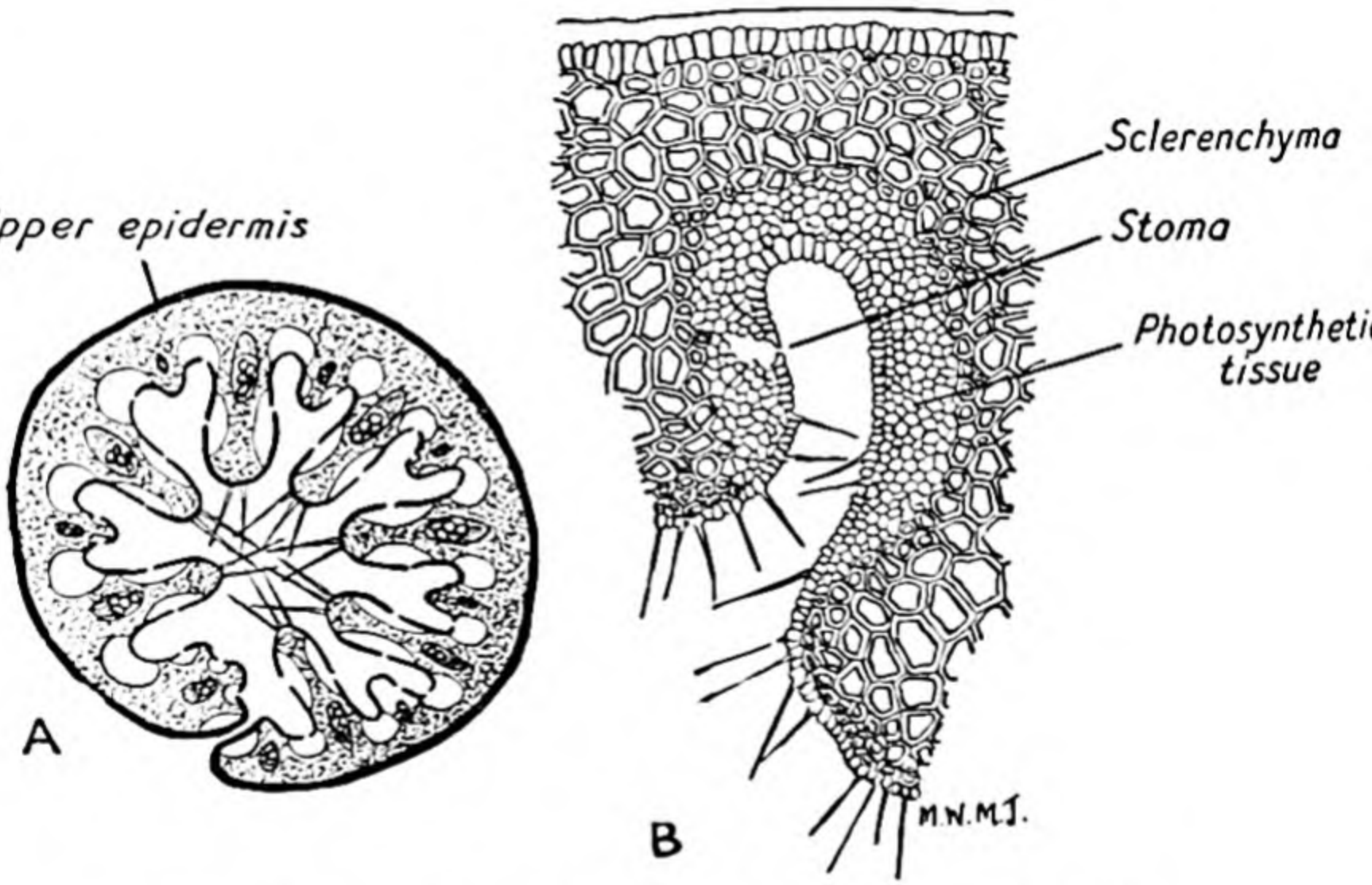


FIG. 352 – Section of the leaf of Marram Grass, a drought-enduring plant. *A*., The entire section; *B*., A single projection further magnified. (After Jepson.)

thick cuticle, whilst the stomata are often protected by being sunk into pits and guarded by hair-like structures. This at once suggests a reduction in the rate of transpiration. Yet the rate of transpiration in these plants is abnormally high, and the various modifications are of no significance in ordinary conditions. They become important only after the loss of water has been sufficient to cause wilting, when they may be effective in preventing desiccation to a degree beyond which the plant cannot

recover. Plants exhibiting these characters possess roots which penetrate into porous soil to abnormally great depths. They have been discovered as far as forty feet from the surface. Consequently rapid transpiration is essential to create sufficient force for the raising of water through such a considerable distance. Very few plants can survive in desert soils, which are so hard as to be impenetrable by roots far below the surface. The so-called creosote bush is an exception, for it can withstand desiccation to such an extent that its protoplasm contains the merest trace of water. The ability of the protoplasm to recover from such conditions is here present to an exceptional extent, though it is probably characteristic of all this type of xerophyte to various degrees.

(*b*) *Succulent Plants*. These depend on the ability to store water, rather than the power to obtain appreciable supplies of it. Within and between the cells of their stems and roots large quantities of mucilage are produced. This imbibes water to such an extent that very little is lost in transpiration. Water is absorbed by shallow roots during any rainy seasons, and its transference to the mucilage enables this process to occur quite rapidly. When drought commences, absorption ceases and the stored supply is utilised. How slow the rate of water-loss can be in a succulent has been shown by the retention, without water, of a cactus, which after six years was found to have lost only one-third of the water it contained at the outset. It is obvious that this type of xerophyte can exist only in conditions where there are occasional rainy periods, so that the supply of water can be then replenished.

(*c*) *Drought Evaders*. This type of plant is not really xerophytic in the true sense, though living in situations normally recognised as arid. Unlike the forms previously described, which are perennials, these are annuals, or even semi-annuals. They appear soon after the commencement of a rainy season, grow rapidly, form flowers, set seed and die off. During the subsequent drought the seeds survive, germinating at the onset of the next rainy period. The frequency of their appearance thus depends on the number of rainy seasons.

Climbing Plants

Most plants have erect stems, although there are some, such as the Ground Ivy, in which the main stem grows along the surface of the ground. To make a stem self-supporting requires materials and time, but if a stem could use some other object for support then it could grow rapidly, and also expend less material in its manufacture. Now some plants have adopted this climbing habit, and it enables them to live successfully in such places as tropical forests, ordinary woods, and along the sides of hedges and banks, where the amount of light is much reduced. These plants are therefore adapted to live in a special habitat, and they are collectively termed *climbing plants*.

The advantages of the climbing habit are –

(1) It enables the leaves quickly to reach the light, so necessary for photosynthesis.

(2) It enables the flowers to be well exposed for pollination and the fruits for dispersal.

(3) The plant can economise in the material used for stem-formation in relation to its own size and height.

Internally, too, the stems show marked adaptation to the particular mode of life of the plants. The food and water pipes are very well developed (often there is internal, as well as external, phloem to the vascular bundles) and they are large in diameter, enabling them to convey the materials over considerable distances fairly rapidly. Also there is frequently developed a ring of fibrous tissue well towards the outside of the stem, imparting maximum strength to the stem with the minimum expenditure of material.

The methods generally adopted for climbing are –

(1) STRAGGLING – e.g., rose, bramble and goose-grass.

(2) ADHESIVE – e.g., ivy.

(3) PREHENSILE – of this there are two categories –

(*a*) *By twining* – e.g., bindweed, honeysuckle, runner bean, hop, black bryony and dodder.

(*b*) *With tendrils* – further classified according to the structure giving rise to the tendrils. Thus there may be –

(i) Main stem tendrils – e.g., Virginian creeper and the vine.

(ii) Axillary (branch) stem tendrils – e.g., white bryony and passion flower.

(iii) Leaf tendrils – e.g., pea and vetches.

(iv) Stipule (outgrowth of leaf-base) tendrils – e.g., *Smilax*.

(v) Leaf-petiole tendrils – e.g., *Clematis*.

Only a few examples of these will be described below.

(1) STRAGGLING – e.g., rambler rose. The stem grows rapidly and after a while it is unable to support itself, so that it falls against any neighbouring support, when the de-curved (bent back) hooks catch in the object and so hold the stem. This is a very simple, unspecialised method (see Fig. 353).

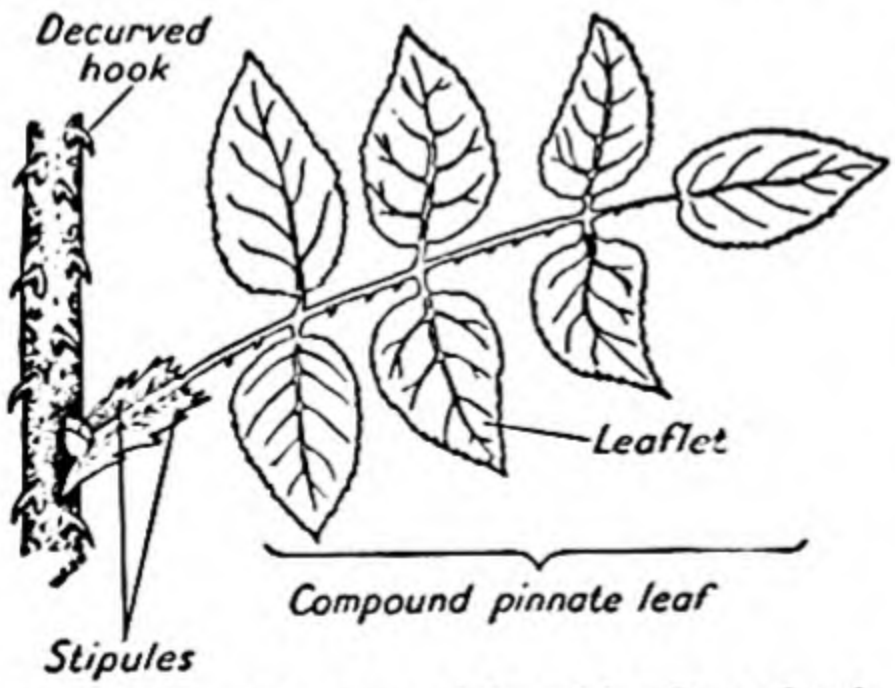


FIG. 353 – Portion of Rambler Rose bush, showing de-curved hooks.

(2) ADHESIVE – e.g., ivy. Although the stem of the ivy becomes woody and may grow to as much as two inches in diameter, it is unable to support itself, but depends on other objects, commonly tree-trunks and walls, for this sup-

port. Adventitious roots grow out from the stem where it is in contact with an object and these roots give out a gummy substance which sticks to the support. These roots are formed mainly at the nodes and grow away from the light. They have no absorptive power. The ivy plant has well-developed roots of its own in the soil and these absorb water and mineral salts in the normal way. This is a more advanced method than the straggling.

(3) PREHENSILE. (*a*) *By twining* – e.g., bindweed. The bindweed stem grows rapidly and climbs round supports in an anti-clockwise direction. The stems die down each year. The bindweed also sends straggling stems along the ground, and these are responsible for vegetative propagation. Twining stems attach themselves by a method entirely different from that adopted by tendrils. The upper part of the stem of a twining plant acquires a horizontal position and slowly rotates on the upright part (this is called *nutation*). On reaching a support this movement is merely continued, resulting in twining about the support. With the exception of the dodder, twining plants are not irritable – i.e., they do not twine as a result of the stimulus of contact. To demonstrate that the twining is due mainly to geotropism, put a young bindweed on to a klinostat and note that it does not form coils. Also invert a runner bean plant and note that the last-formed coils will uncoil and then re-coil in the opposite direction.

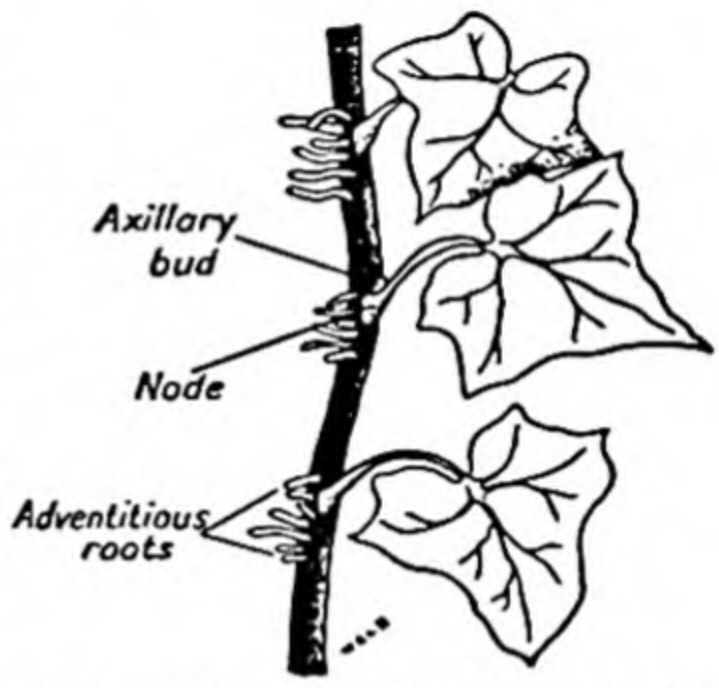


FIG. 354 – Part of an Ivy plant. Note that the adventitious roots arise mainly at the nodes and grow away from the light.

In the temperate zones twining plants are mostly herbaceous annuals (the hop and honeysickle are exceptions to this), but in the tropics and sub-tropics many are woody.

The bindweed, as stated previously, and the runner bean twine in a counter-clockwise direction, but the honeysuckle, hop and black bryony twine in a clockwise direction.

(*b*) *With tendrils*. (1) Main stem tendrils – e.g., Virginian creeper. The main stem forms tendrils, so that the growth of the plant has to be carried on by axillary branches. The tendrils form, at their ends, little sticky discs which hold them to the support, so that this plant combines the prehensile and adhesive methods. If the disc does not meet a support the tendril curves, but it does not twine thoroughly unless it receives a stimulus of contact. The tendrils are mainly negatively phototropic – i.e., they grow away from the light. (2) Tendrils from leaf-petioles – e.g., *Clematis* (Old Man's Beard). This plant belongs to the buttercup family

and has white, mauve or red flowers, which have no petals (the structures which look like petals are actually sepals) and produce no nectar, but insects visiting the flowers are rewarded with pollen. It is a perennial plant and its stem grows in thickness, becoming woody. The petioles of the compound leaves coil only slightly, remaining non-woody and rather thin, if they do not touch a support. If they do touch a support the stimulus of contact causes them to coil tightly round it, to grow in thickness and to become woody.

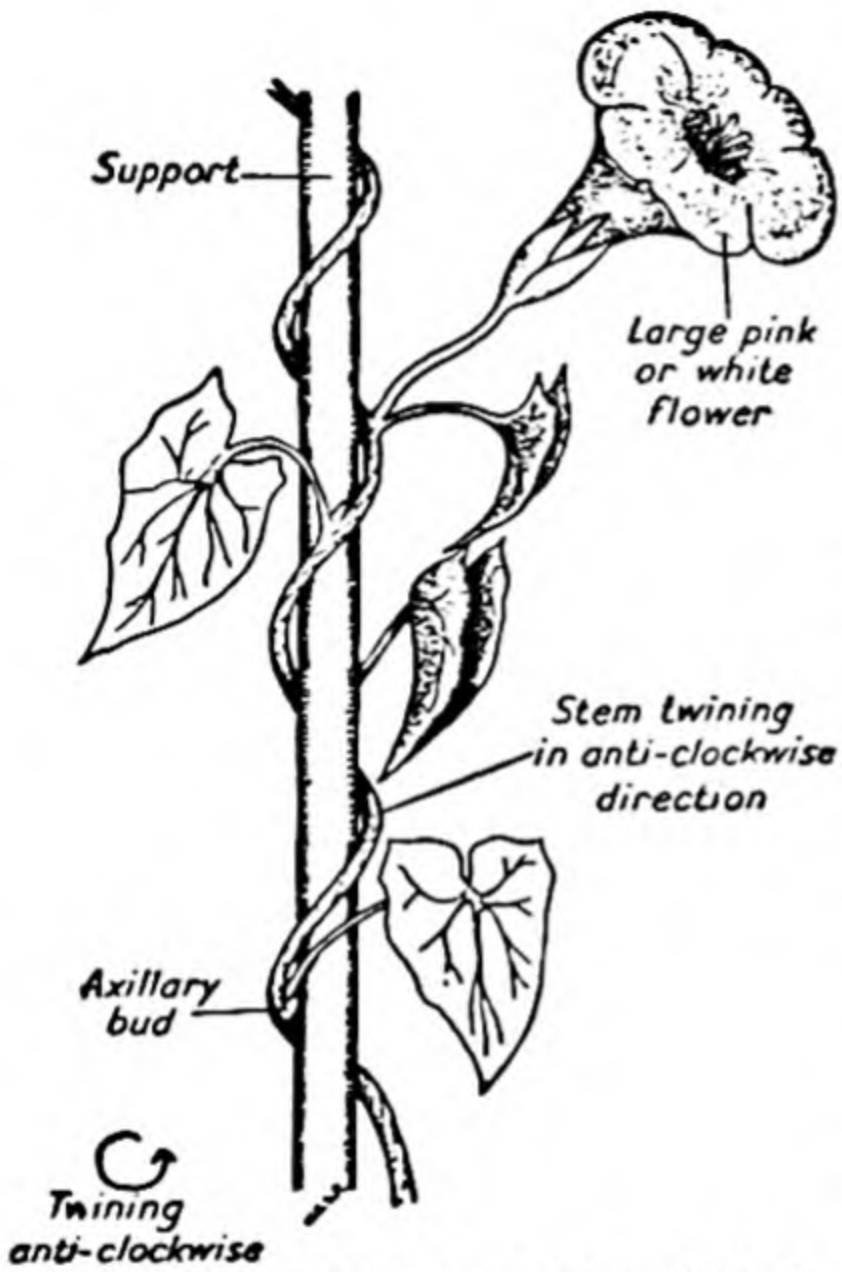


FIG. 355 – Bindweed (*Convolvulus*).

Tendrils show two kinds of movement – (1) a slight twining, which takes place in the absence of any contact with external supports and which is due to internal causes, resulting in the accelerated growth of the tendril on various sides, and (2) the clasping of the support when suitable contact is made. This is actually a tropism, the stimulus of contact causing the accelerated growth of the side of the tendril away from the support. Contact with a solid body is necessary; water or mercury will not cause curvature. If the stimulus is weak or of short duration the tendril will straighten out again. Contact not only causes curvature at the spot touched, but the impulse is conveyed to other parts of the tendril, which are also stimulated to thicken and to lay down a considerable amount of mechanical tissue. The capacity to perceive the stimulus is localised almost exclusively in the concave (ventral) side, and a touch on the dorsal side will produce no curvature. In many, but not all, plants there are present, at the sensitive part of the tendril, special cells, provided with pores, which may be related to their property of sensitivity. The pores consist of minute canals in the external membrane of the cells and are filled with protoplasm. Thus it will be seen that climbing by means of tendrils is the most advanced method.

Plants with Unusual Nutrition

The typical green plant uses simple inorganic substances, namely carbon dioxide from the air, and mineral salts and water from the soil, and it builds these up into complex, organic substances, including sugar,

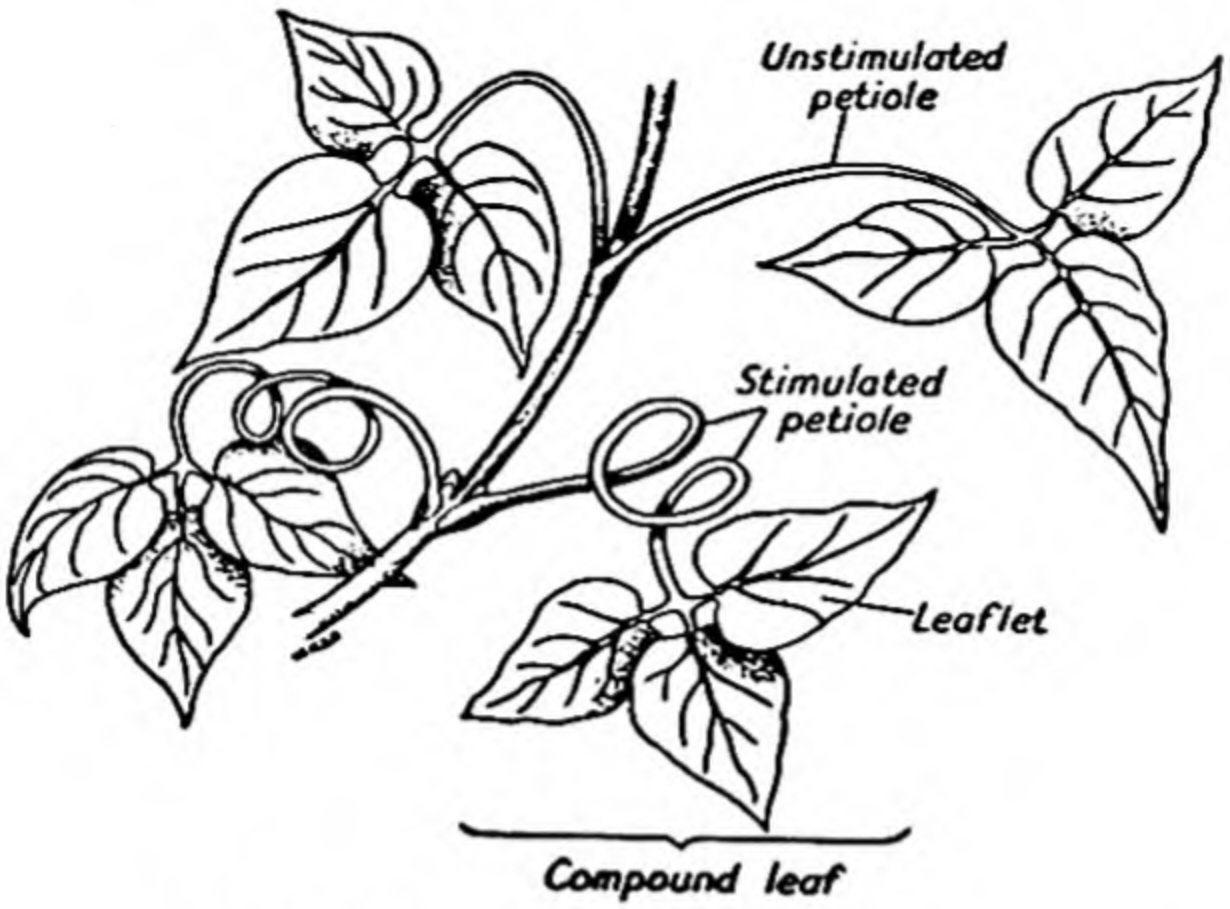


FIG. 356 – Part of a Clematis plant.

starch, fats and proteins. Animals, on the other hand, must have these complex organic foods ready made, and cannot manufacture them. They obtain them either by eating green plants or, indirectly, by eating other animals which themselves ate green plants. In the book of Isaiah we read 'All flesh is as grass'. This, then, is a profound biological truth, providing 'grass' be taken to imply all green plants. Now some plants have lost their chlorophyll, the green substance which enables them to utilise the energy of light to build up carbon dioxide and water into sugars and starch, so they have to feed rather like animals, and have these complex foods ready made. They can either obtain this complex food from dead matter, when they are termed saprophyes (e.g., yeast, *Mucor*), or they can obtain it from other living plants (or animals), when they are termed parasites.

THE DODDER, or *Cuscuta*, is an example of a parasite, and because it lives on the outside of another plant it is called an *ectoparasite*. Although this plant is dealt with much more fully subsequently (page 667), it is desirable that its principal features should be noted in this present context. There are three native species of this plant, the following description applying to the Lesser Dodder, parasitic upon such plants as hops and furze.

It is a perennial plant and its seed germinates in late spring after its hosts have already developed. It sends out a little root into the soil to absorb water, and a stem which sweeps round and round at the

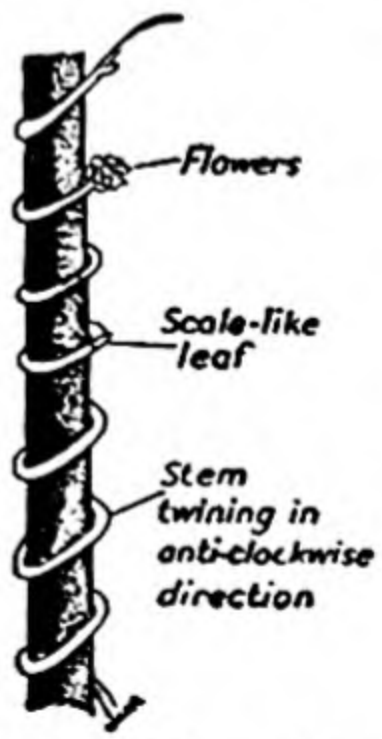


FIG. 357 – The Dodder plant.

tip in an anti-clockwise direction. If this stem does not come into contact with a host plant stem, then the little dodder plant soon dies, once it has used up the food stored in the seed and it cannot make any more. If this stem does meet a host stem it twines closely round it and sends into it little disc-like absorbing organs, called *haustoria*, or suckers. Each haustorium produces cells which connect the xylem and phloem of the dodder with those of its host, so that water, mineral salts and complex organic food can be absorbed from the host into the dodder. The haustoria penetrate the host stem by combined pressure and enzyme action. Once the dodder has established itself on the host plant its own root dies away.

The stem of the dodder is just a little thicker than a piece of cotton, and is pinkish when young, but becomes brown in the older parts. It bears spirally-arranged leaves, but they are reduced to little scales, and later on, in about July or August, there appear in the axils of these scales little clusters of pinkish flowers. Although the flowers are so small, each one has sepals, petals, five stamens and an ovary formed from the bases of two carpels. The stem of the dodder is irritable to contact.

The dodder is thus adapted to its special mode of life. (1) It has haustoria for absorbing food from the host. (2) There is a reduction of xylem in its stem, but this is no disadvantage, since it has not the ordinary full functions to carry out. (3) The leaves are reduced to scales, no longer used to make food. (4) It produces a large number of small flowers, each giving rise to four fairly large seeds. (5) The ovules and embryos are very simple. (6) Germination of the seed takes place in the late spring when the host plant has already developed. Because it is entirely without chlorophyll it is described as a *total* parasite.

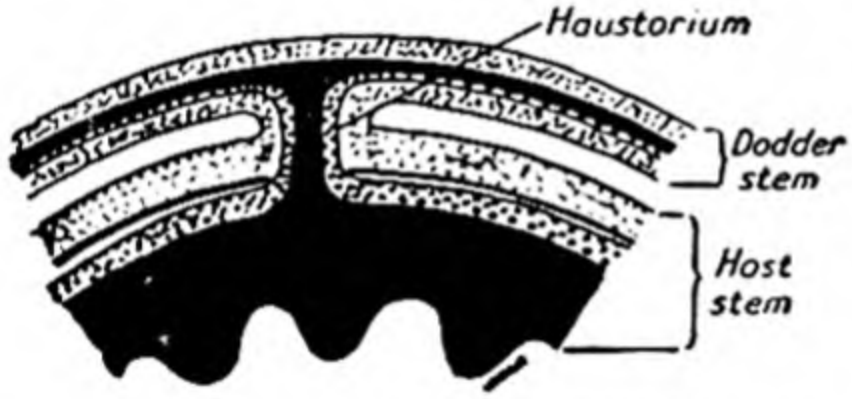


FIG. 358 – Diagrammatic transverse section of the stem of a host plant, with haustorium of the Dodder.

Amongst British plants there are many *partial* parasites. They are green and can therefore make sugar, but they supplement their food-supply by absorbing manufactured food (and raw materials) from a host plant. Examples of these plants are to be found in the toothwort and the yellow rattle, as well as the mistletoe, all of which establish nutritive connexion with suitable host plants. Thus the toothwort is found commonly on the beech and hazel, the yellow rattle on grasses and the mistletoe on apple trees.

There is yet another group of green plants which supplement their food-supply in a very interesting way. They capture insects, digest them and then absorb the complex organic food which makes up their bodies. In this manner they obtain an abundant supply of nitrogen-containing

compounds. In tropical and sub-tropical countries larger and more numerous kinds of insectivorous plants are to be found, some well-known ones being Venus' fly-trap and the pitcher plant.

In Britain there are only three genera of these plants. They are small and easily passed by unless a special effort is made to locate them. They are (1) *Drosera*, the sundew; (2) *Pinguicula*, the butterwort, and (3) *Utricularia*, the bladderwort.

THE SUNDEW (*Drosera*). This plant is generally to be found in situations where the supply of available nitrogen is low – i.e., in boggy fields. It is a perennial plant, flowering in July and August. The flowers are small and regular, with five persistent sepals, five petals, five stamens and one carpel. It has ordinary roots in the soil, but the stem is very short, so that the leaves all appear to come off together in a rosette right on the ground. In one species the leaves are oblong and in another obvate (oval, but with the greatest diameter towards the tip of the leaf). These leaves contain chlorophyll, so that they can make sugar, but they look reddish because they are covered on the upper surface with red, glistening hairs. These hairs are composed of a stalk and a head and are very specialised structures, secreting (1) a sticky material, (2) digestive juices

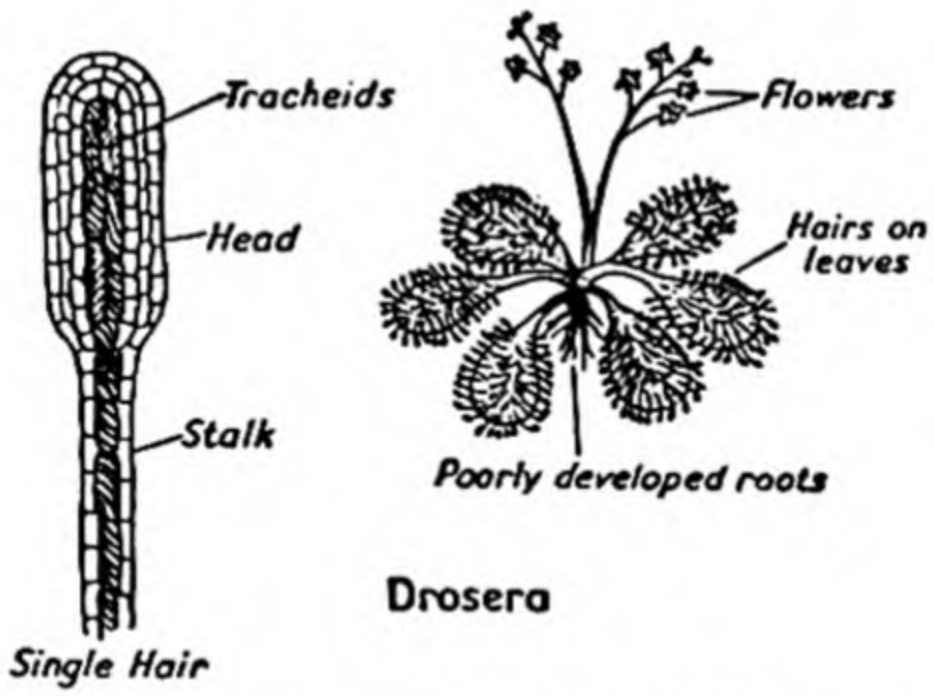


FIG. 359 – The Sundew (*Drosera*).

(enzymes), and (3) an acid. If an insect lands on the leaf it sticks to the hairs. This causes an impulse to be sent to the other hairs on the leaf, and they respond (i) by bending over towards the insect, and (ii) by secreting enzymes and acid on to the body of the insect. It is believed that the enzyme is pepsin, but that the acid is a member of the fatty acid series. The hairs secrete the sticky substance without being stimulated, but they produce enzymes and acid only in response to stimulation. They are very sensitive and it is claimed that a single human hair, 1/78,740 gm. in weight, is sufficient to stimulate them. The digested products of the insect are absorbed by the hairs. When digestion is finished the hairs uncurl,

becoming dry for a while, and in this state they will not respond to the stimulus of another insect. Later they become sticky and regain their powers of response.

Drosera is, of course, found in parts of the world other than Britain and the plants are very much larger. In Australia, for example, *Drosera binata* has a stalk 20 inches long and a leaf-blade 7½ inches long. The blade of the British round-leaved species (*Drosera rotundifolia*) is only about half an inch in diameter.

THE BUTTERWORT (*Pinguicula*). This is also found in boggy places, especially on the lower slopes of mountains. There is quite a lot of it in Wales, and at Port Talbot it can be found on the sandy stretches between the sand dunes and the sea, quite close to the latter. Here, again, there are normal roots and a very short stem, with the fleshy, oblong, green leaves (about 1½ inches by ¾ inch) forming a rosette pressed quite close

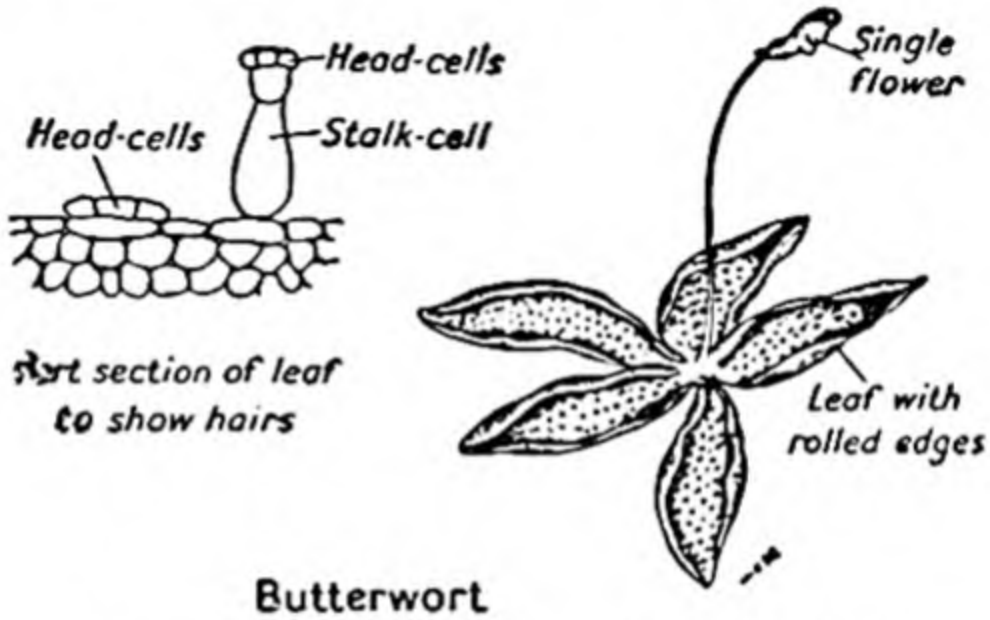


FIG. 360 – The Butterwort (*Pinguicula*).

to the ground. The margins of the leaves are incurved and the upper surface is thickly covered with two sets of glandular hairs – (1) larger ones, consisting of a unicellular stalk and a head of 16 radiating cells, which secrete a viscid fluid, but no enzymes, and (2) smaller ones, with half the number of cells in the head, no stalk, and of paler colour; they secrete a fluid containing enzymes. The sticky substance is secreted continuously, so that the hairs glisten, but they give out enzymes only when stimulated by nitrogenous bodies, and this stimulus also causes the margins of the leaf to curl further inwards. The margins remain closed for a short time – 24 hours or less – and this curvature may be induced by mere pressure.

About May to July it produces a single flower on the end of a fairly long stalk. It is blue in colour and resembles a small violet.

THE BLADDERWORT (*Utricularia*). This insectivorous plant is a hydrophyte – i.e., it lives in water. The plant has no roots at all, simply floating in the water. It produces yellow flowers above the water. The leaves are compound and very much dissected, rather like the waterleaf

of the water-buttercup. Parts of the dissected leaves are modified to form bladders. Each bladder has a valve, resembling a trap-door, to guard its opening, whilst attached to, and in front of, this valve are some transparent bristles. Inside the bladder are the so-called digestive glands,

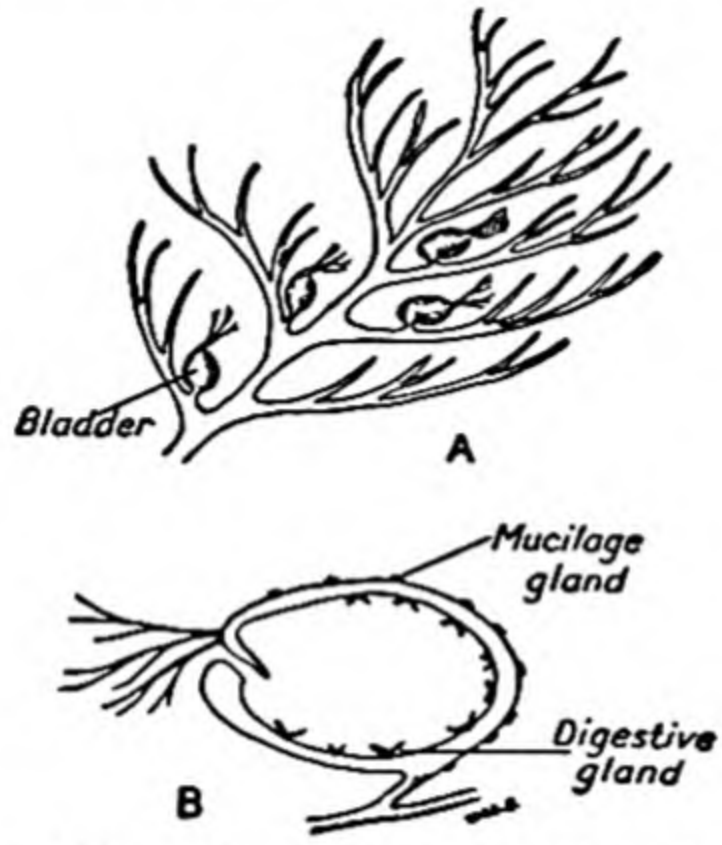


FIG. 361 – The Bladderwort (*Utricularia*).

each of which consists of a basal cell and a branched head. These 'glands' do not produce enzymes, but are largely absorptive in function. Scattered on the outside of the bladder are mucilage glands, each consisting of a stalk and a head of two cells.

The cells lining the bladder absorb some of the water within, so that the bladder partially collapses. If a water-insect now touches some of the hairs in front of the valve the valve is caused to open (inwards), so that water, with any insects it may contain, is drawn into the bladder, after which the valve closes again. The insect dies inside the bladder and its body is decomposed by Bacteria, after which the soluble products are absorbed.

Conclusion

The main principles of adaptation of animals and plants to environment have been dealt with above, but it is beyond the scope of this book to pursue this subject in detail. Ecology – the study of animals and plants in relation to environment – is very greatly regulated by local conditions, for it, like other branches of biology, is essentially practical. Thus the ecology of plants may be considered in connexion with woodlands, marshes, heaths and moors, water or the seashore, according to which is most readily accessible. The numerous text-books available will supply all the information required regarding the ecology of the selected community. A short list of suggested books is appended.

BIBLIOGRAPHY

Animal Ecology, by Charles Elton. Sidgwick and Jackson.
Plant Ecology, by J. E. Weaver and F. E. Clements. McGraw Hill Book Co.
Practical Plant Ecology, by A. G. Tansley. Allen and Unwin.

PRACTICAL WORK

In addition to the experiments described in the text of this chapter several other experiments on soil may be performed with advantage. The student is referred to the new edition of *Simple Experiments in Biology*, by Cyril Bibby (Heinemann). This excellent book will also be found of great service in many other branches of practical work.

CHAPTER 39

The Animate Environment

The relationship between animals and plants may be considered from a number of aspects, each differing from the other in extent, rather than in the principle involved. The same is largely true of the relationship of one animal with another and of plants amongst themselves. Fundamentally the whole assemblage of living things is unified through the mutual relationship established in connexion with nutrition. The energy available to all living organisms is necessarily derived, directly or indirectly, from that of the sun. In this respect animals and plants may be considered collectively.

Energy of Living Organisms

The nearest approach to the direct utilisation of the sun's energy is evident in the process of photosynthesis, though it is now established that part only of this complicated series of reactions is photochemical. As a result of this and allied processes complex chemical molecules are built up, so that much potential energy is stored. Part of this becomes converted into kinetic form to facilitate growth and other active life-processes in the plant, and such production of energy is sometimes evident externally, as, for example, in the rise of temperature during the germination of seeds. But more important is the role played by plants in affording the food of herbivorous animals, in whose bodies a great deal of the stored energy of the complex molecules is liberated in the performance of work. Carnivorous animals in their turn prey upon herbivores, so that they depend indirectly for their existence on the plants which afford the food of their prey. Thus what are known as food-chains may be established, emphasising the continuity of energy-distribution. Thus if animal *A* feeds on animal *B*, which in its turn preys on animal *C*, itself herbivorous, then animals *A* and *B* will each depend on the plants which provide the food of animal *C*. These plants are continually fixing energy from the sun through the process of photosynthesis. Thus, for example, the energy required by a greyhound to chase an electric hare is derived as a result of a series of transformations of the light-energy of the sun. Grass and grain may provide the stable diet of the cattle whose flesh is fed to the greyhound, part of whose body-substance is oxidised with the liberation of mechanical energy. It would appear at first sight that a very great deal of energy must be continuously lost, since on the face of it no sort of replacement is apparent. In effecting

movement heat is produced, and thus energy is liberated. It is the same with all forms of energy: one form may be converted into another, but the total of energy remains unchanged. This is known as the Law of Conservation of Energy. Thus coal consists of fossilised plant remains, and as such contains supplies of potential energy derived largely as a result of photosynthesis. The coal may be burned, yielding heat and light energy, or it may be used to drive a dynamo, and hence be converted into electrical energy. It is true that the amount of energy on the earth is continuously increasing, as more is being stored in the form of the potential energy of the molecules of protoplasm of animals and plants. But such energy has been obtained from the sun, whose own store of energy is continuously decreasing as a result of the extremely rapid disruption of its substance. It is really true only of the universe as a whole that the energy-content remains constant, and even this involves the acceptance of the belief that matter and energy are interchangeable.

Gaseous Relationships

The circulation of carbon in nature has already been described (page 410). Animals liberate a great deal of carbon dioxide in the process of respiration, for which they absorb large quantities of oxygen. Plants, on the other hand, though they respire slowly, are primarily concerned with the intake of carbon dioxide for the performance of photosynthesis, a process accompanied by the evolution of oxygen. Thus between them an extremely important equilibrium is established, whilst each is therefore essential to the continued life of the other. Plants are very largely responsible for the circulation of nitrogen, and in this connexion the Bacteria of the soil are particularly significant. Reference should be made here to the nitrogen cycle (page 410), wherein the mechanism of this circulation is depicted diagrammatically.

Food Relationships

It has already been pointed out that all living organisms are mutually dependent upon one another through food-supply. This is especially evident where localised areas are considered, and would account for the geographical distribution of animals and plants. Climatic conditions in the first place regulate the distribution of plants, and in this respect intensity and duration of light seem to be the most important factors. It has frequently been discovered that the vegetative growth is not seriously impaired by the cultivation of certain plants in latitudes far removed from those of their normal habitat, but flower- and fruit-formation have become largely or entirely suppressed (page 421). Thus in natural conditions they become confined to certain regions. Consequently the herbivorous animals of which they form the staple diet will to some extent become similarly restricted. This will in turn regulate the distribution of

other animals whose food is provided by the herbivores in question. Animals are themselves influenced by climatic conditions, becoming variously adapted. Thus the coats of arctic mammals are normally thick in texture and white in colour. The former is responsible for the imprisonment of a wide layer of air, a notably bad conductor of heat, whilst a white surface loses heat by radiation more slowly than a black one, so that a good deal of heat is prevented from escaping from the body, thus conserving body-temperature. Evolutionarily the distribution of both animals and plants may be regarded as a triumph of adaptation to environment. Animals and plants structurally and physiologically suited to their surroundings have survived, and no greater differences than would be expected exist between them. Indeed in a given habitat there is often a marked uniformity in the structure of the animals and plants, so much so that, though their evolutionary histories may be quite widely different, the various animals or plants resemble one another quite closely. Examples of such convergence of structure are provided by whales, which simulate fish in external form, whilst some Amphibia and reptiles have independently assumed a snake-like form. All the Alpine cushion plants are superficially alike, though belonging to widely different orders. Survival has depended not only on successful adaptation to climatic conditions, but also on the ability to utilise available foods, in which connexion animals and plants have become intimately related. Barriers to distribution have already been mentioned (page 603). Civilisation has had considerable influence upon the distribution of animals and plants, but the natural fauna and flora are sufficiently represented for the diagnostic features of regional distribution to remain clearly indicated.

Individual Relationships

So far only those relationships which involve either animals and plants collectively, or at least large groups of them, have been considered. It remains to discover to what extent association between individual organisms has been established, and with what results to the participants. Such individual associations may be divided into three classes, each of which may be regarded as evolutionarily connected with the others.

(A) COMMENSALISM. This term, applied to a certain type of association between living organisms, means literally 'feeding at the same table'. It may be taken to imply a loose association of organisms, which share food and environments without the one injuring the other, which would be a form of parasitism (see later). An example of it in animals is provided by the suck-fish (*Echeneis*), frequently found attached to the ventral surface of the dogfish. Attachment is effected by means of the dorsal fin of the suck-fish, for this structure becomes modified to form a sucker. The suck-fish is sufficiently small not to inconvenience the dogfish, whilst it itself is carried rapidly about the ocean and thus is more likely to acquire supplies of food. Further, since the dogfish is a voracious

feeder, it is also a waster, so that sufficient food may be provided for the suck-fish in this way.

A further example, showing how the association may benefit the two or more associates, is afforded by the hermit crab, *Eupagurus*, and its commensals, which are the sea-anemone (*Adamsia*) and possibly *Nereis fucata*, a marine annelid. *Eupagurus* normally seeks shelter in the empty shell of a mollusc, such as a whelk, and it is to this that the anemones become attached. The crab is almost continuously scraping up portions of sediment from the sea-bottom, and this material is sifted in its outgoing respiratory current. It thus discharges a cord of sediment, rich in micro-organisms, which provide suitable food for the anemone. The scraping movement of the shell must frequently disturb such animals as small crabs and polychaets, and these supplement the food-supply of the anemone, whilst a further source is provided by the fragments liberated when the crab is tearing up larger animals for use as its own food. At the same time the anemone provides protection for the crab against attacks by other animals, owing to the fact that its nematocysts render it distasteful. Within the shell inhabited by the hermit crab may frequently be found *Nereis fucata*. The fact that the crab is slow in dealing with large food enables the worm to emerge from the shell and seize portions of the food, and this may actually be of benefit to the crab if the food is of such a size and nature that the mouth parts cannot readily manipulate it. In any case it is not detrimental to the crab unless food is scarce. The undulating movements of the worm within the shell may possibly assist in the renewal of water, and thus prove of considerable benefit to the respiratory process of *Eupagurus*.

The nearest approach amongst plants to the condition of commensalism amongst animals is provided by certain plants collectively termed **epiphytes**. These obtain a more plentiful supply of light by establishing themselves on the branches of trees, instead of being rooted to the ground. But their problem of nutrition is difficult, since they do not actually penetrate the tissues of the tree to which they are anchored, but may become attached equally readily to inorganic substrata. In this respect they differ fundamentally from parasitic plants. The obtaining of water and salts is accommodated by various structural modifications. In many instances they exhibit xeromorphic characters, having structures adapted to the retention of water. In the aerial roots of some orchids, for example, the epidermis and outer cells of the cortex become specially absorbent, constituting the **velamen**. In others the roots are directed upwards and branch to form a cup-like structure, in which falling leaves are caught and converted into humus. Bacterial action on this, as in the soil, results in the formation of nitrates, absorbed by the plant. Certain tropical ferns behave similarly, though here it is the leaves which serve to collect humus and water. Such associations are obviously closely similar to the commensalism of animals, though in plants they result in

the fulfilment of an essential condition – i.e. an abundance of light – and not in a ready means of access to food, as is normally the case in animals.

(B) PARASITISM. This association between two organisms involves considerable benefit to the one, whilst harmful, or even fatal, effects may be exerted upon the other. Sufficient instances of this phenomenon in animals have already been given, whilst amongst plants the parasitic nature of *Pythium* and many Bacteria has been noted. It remains therefore to consider the resort to parasitism of some higher plants, and of the consequent effects upon their structure. The dodder (*Cuscuta*) may be taken as an example. There are many species of this plant, the commonest being *Cuscuta europoea*, parasitic upon nettles (especially in moist situations, such as river banks) and upon hops, and *Cuscuta epithymum*, found associated with gorse, broom, heather and clover. From a structural point of view there is close similarity between members of the various species, but the restriction of each to a relatively small group of hosts denotes a high degree of physiological specialisation. The stem is thread-like, entwining the host plant. The leaves are represented by minute scales, completely devoid of chlorophyll and separated by long inter-nodes. At intervals along the stem arise suckers, or **haustoria**, penetrating the tissues of the host. There is no root, so that the parasite is utterly dependent upon its host for food. The xylem is especially poorly developed, whilst the haustoria at first consist of undifferentiated cells. These later become modified, those continuous with the xylem of the host assuming the form of tracheids, whilst those in contact with the phloem simulate this tissue. It is in the matter of life-history that pronounced specific differences are encountered.

Cuscuta europoea gives rise in the autumn to a large number of seeds, whose dispersal may be aided by flooding. Germination takes place in the following May, giving rise to a free-living stage, in which, however, no clear division into root and shoot is apparent. During the growth of this slender plant extensive nutating movements occur, thus increasing the prospects of contact with a suitable provisional host, which at this stage may be a grass or some small seedling. After a brief 'settling down' period growth becomes very rapid and may well result in numerous contacts being made with the major host (nettles). Where these contacts occur haustorial penetration will take place, though it would appear that a plentiful supply of moisture is necessary for this process. Flowering commences in July. Pollination is normally effected by insects, though the possibility of self-pollination and even cleistogamy cannot be ruled out. The plant is essentially an annual, with seeds providing the sole means of survival.

Cuscuta epithymum differs in several respects in the matter of its life-history, the most significant being its habit of perennation. Its seeds germinate somewhat later than the simultaneously dispersed seeds of its host, thus practically ensuring the existence of suitable seedlings upon

which the young dodder plants may become parasitic. Haustorial penetration occurs in moist situations, normally into the cotyledons or first foliage leaves of its host. The infected seedling soon dies, but by this

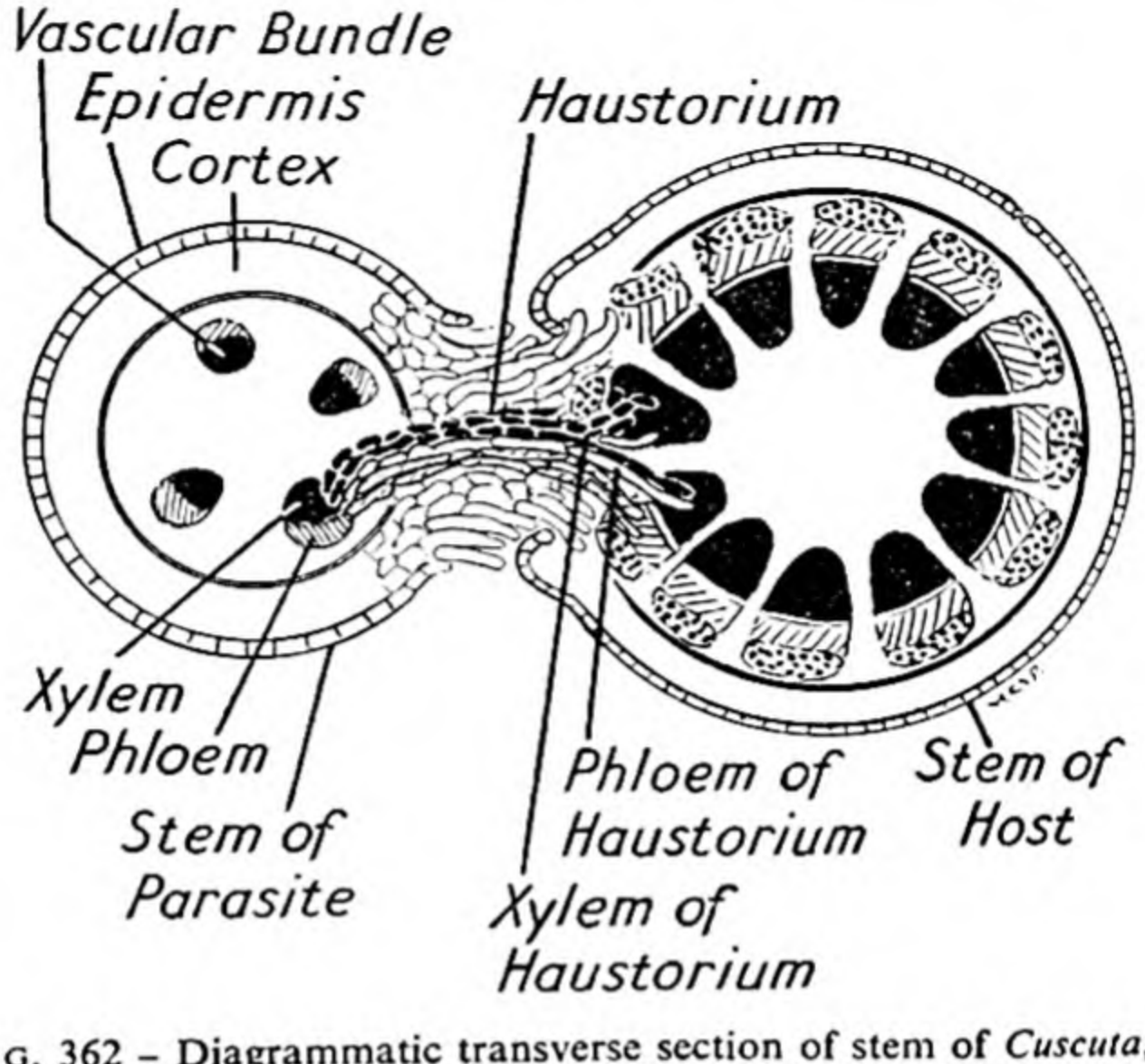


FIG. 362 – Diagrammatic transverse section of stem of *Cuscuta*, with host stem and haustorium.

time the parasite has become sufficiently developed to be able to attack a small gorse bush, after which a period of very rapid growth facilitates the spread of the parasite over a wide area. It is believed that no flowers are produced in the first year, but that in the autumn, when most of the stems of the parasite die off, small swollen tubercles survive, closely adpressed to the host stem. It is from these tubercles that growth is renewed in the following spring. It would appear that this type of winter survival of the parasite can continue as long as the life of the host lasts, and thus this species of *Cuscuta* is strictly perennial, a valuable attribute when it is appreciated how great are the chances against successful germination of seeds in such an environment. For further reading on this subject the reader is referred to the article on 'Dodders' by James F. Shillito in the *School Science Review*, No. 121 (John Murray), from which article the author derived much valuable information.

The dodder is remarkable even amongst parasitic plants in possessing no root. Others – e.g. the broomrape (*Orobanche*) – have roots which become intimately connected with those of the host plant, whilst the shoots remain independent. Similar features are exhibited by the toothwort (*Lathroea*).

(C) SYMBIOSIS. This final type of association is characterised by the reciprocity of benefit to the symbionts. The commonest example of this phenomenon is the presence of non-cellular Algae in certain animal cells.

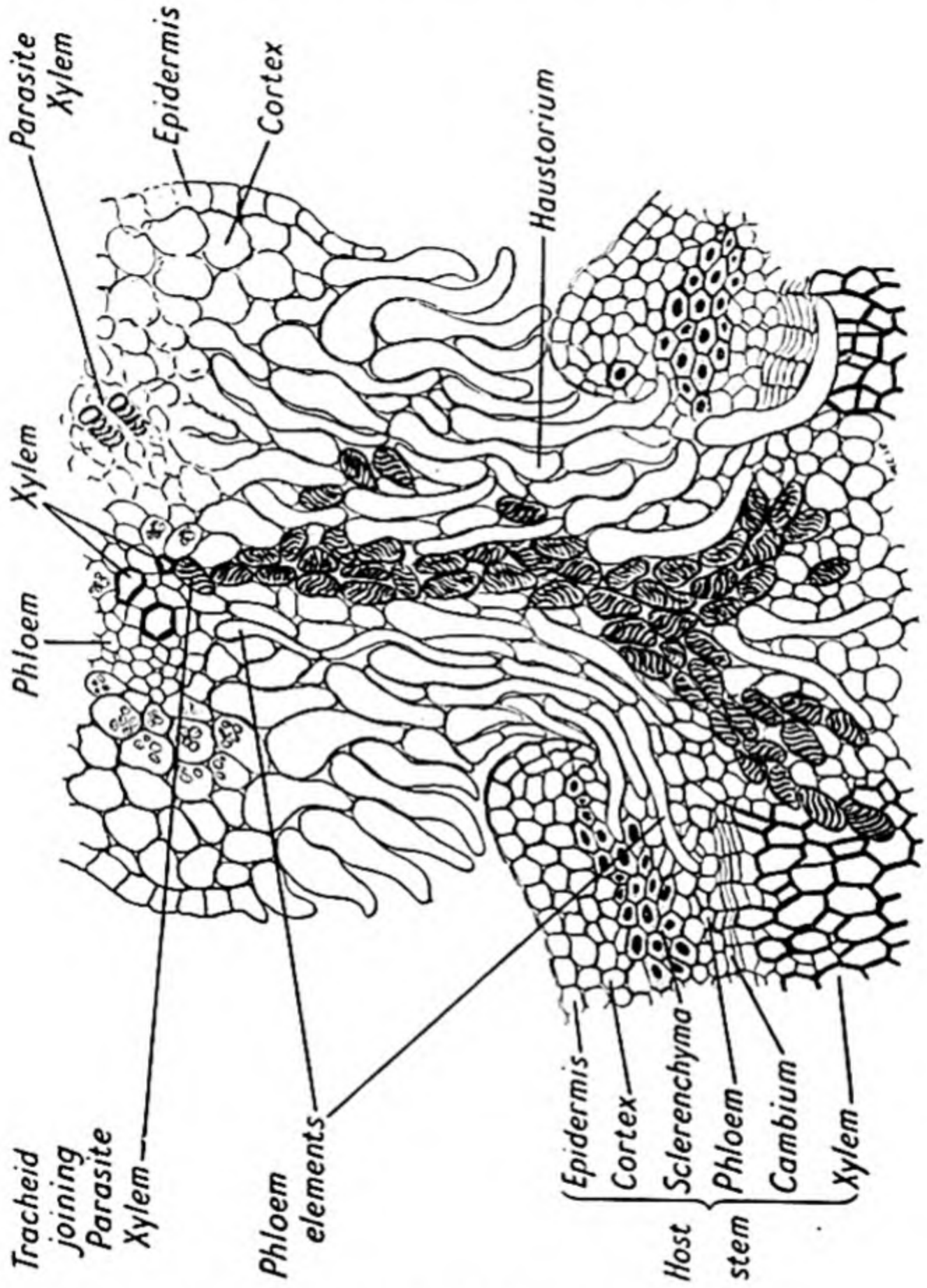


FIG. 363 – High power section of haustorium connecting *Cuscuta* with host stem.

These Algae are known as Zoochlorellae and Zooxanthellae, and they are common in Coelenterata, exemplified by *Hydra viridis*. Being of typical plant structure, these cells photosynthesise sugars from water and carbon dioxide. The latter constituent is provided as a result of respiration by the animal, whilst the oxygen liberated in photosynthesis assists in the animal's respiratory process. Nitrogen- and phosphorus-containing waste products from the animal are utilised by the plant inclusions, whilst

the excess of these elements over and above what the plant requires is reconveyed to the animal in an assimilable form. In practice, however, a certain degree of independence is retained by either or both symbionts, as shown in the following examples.

Convoluta, a marine genus of free-living flatworms (class Turbellaria), exists in two specific forms – *C. paradoxa* and *C. roscoffensis*. Each contains Algae in its constituent cells. *C. roscoffensis* in early life is a voracious feeder, but later loses the power of taking in solid food and eventually ingests its own algal inclusions before dying. *C. paradoxa* knows no such abstemious fits, but feeds holozoically throughout life. Both species at birth are colourless, and so they remain if reared in carefully filtered water. But these forms never attain maturity, dying apparently of nitrogen and phosphorus starvation. The importance of these algal inclusions with regard to metabolism of compounds of nitrogen and phosphorus is further emphasised by the fact that these coloured *Convolutae* possess no excretory organs. Thus *C. roscoffensis* has become too degenerate as a result of symbiosis, and in losing its powers of feeding holozoically it has cast too great a burden on its algal inclusions; the whole therefore dies. *C. paradoxa* actually retains a considerable degree of independence. Infection is normally effected by the inclusion of Algae in the egg-capsules. Since the eggs are laid in conditions of darkness the algal inclusion remains at first colourless, its pigment being developed only on exposure to light.

In the above examples it will be clear that general physiological processes have become specialised, so that the character exhibited may be regarded as physiological adaptations. Now life-processes must be accommodated by structures possessed by the organisms in question. It follows therefore that physiological adaptations must be regarded as evidence of the existence of anatomical adaptations. The loss of the power of independent existence by the algal inclusion of *Convoluta* may be due to nuclear degeneration, or merely to the inability to synthesise sufficient protein from the low concentration of nitrogen- and phosphorus-containing salts in sea-water. The species of *Convoluta*, on the other hand, present adaptations in their nutritive and excretory processes.

The symbiotic association between some herbivores, such as the rabbit, and the cellulose-digesting Bacteria present in their caeca has already been referred to (page 391). There is a further somewhat similar example recently investigated in tame rabbits. During the night soft, mucus-coated droppings are taken by the lips from the anus and passed a second time through the alimentary canal – a process known as *refection*. The droppings deposited during the day are characteristically harder and dry. It is believed that symbiotic Bacteria in the caecum (i.e. after the absorptive region) modify vitamin B_1 in such a way that it can be more readily absorbed into the blood-stream, and that this does, in fact, take place during the second passage of this portion of the food through the

gut. The position is reversed in wild rabbits, which feed largely at night.

Symbiosis is represented in plants, and may be first exemplified by the **Lichens**. A Lichen consists of a dense Fungus mycelium containing algal cells, and occurs commonly on tree-trunks, walls and the surface of soil. The thallus is normally discoid or lobed, but sometimes is branched. Examples of the former are provided by *Xanthoria* and *Parmelia* and of the latter by *Usnea* (see Fig. 364). The Algae appear to show no difference

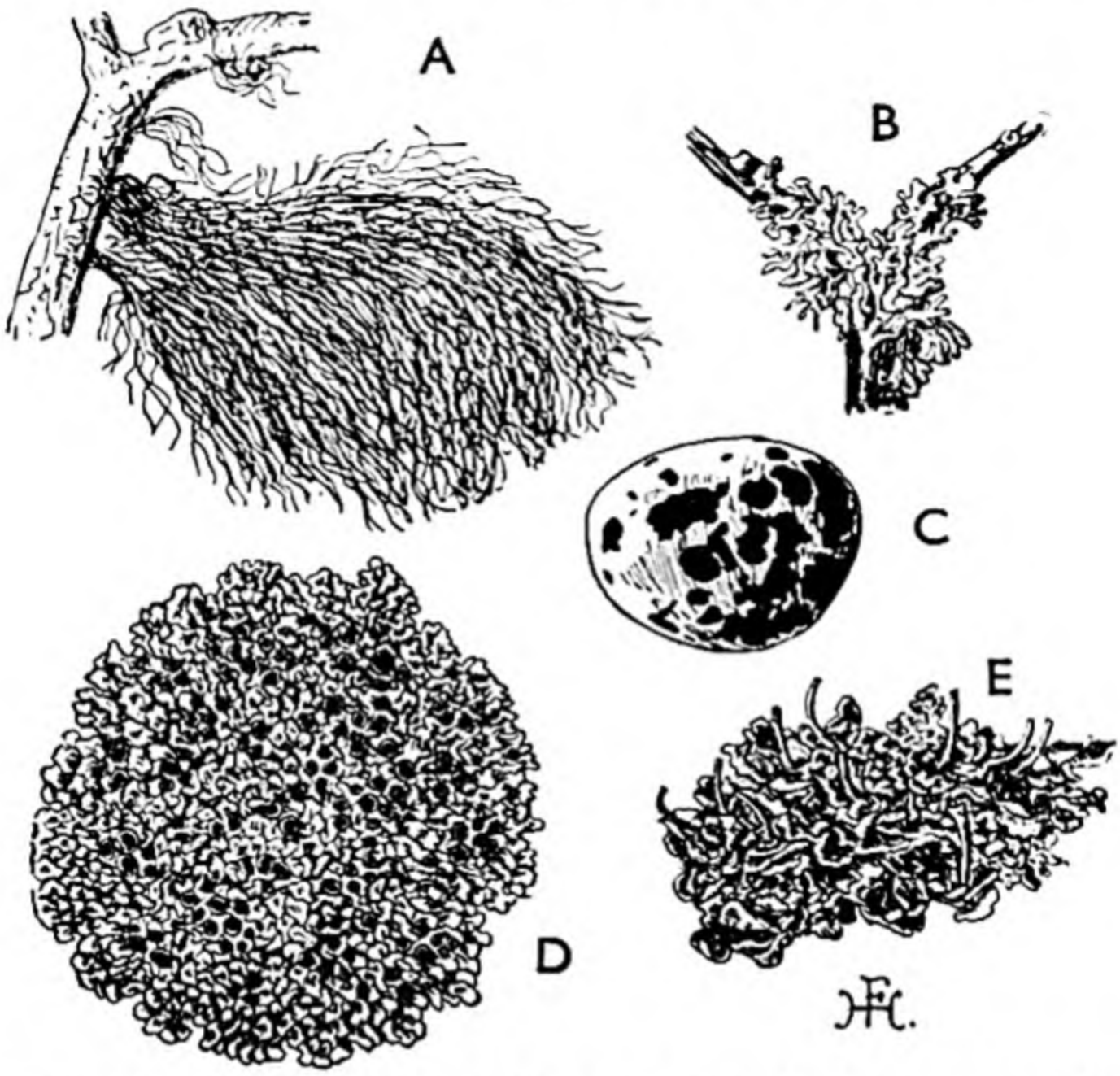


FIG. 364 – Various common Lichens. *A.*, *Usnea barbata; B.*, *Parmelia physodes*, on twig; *C.*, *Rhizocarpon confervoides*, on pebble; *D.*, *Xanthoria parietina* (showing numerous apothecia); *E.*, *Cladonia* sp., showing the upgrowths on which the apothecia are borne. (From *Plant Form and Function*, by F. E. Fritsch and E. J. Salisbury. Bell.)

from those living freely in terrestrial situations, though there is no doubt that they derive benefit from the association. The Fungi, on the other hand, are unable to exist except each in association with its particular Alga. Thus the green *Trebouxia* occurs in the Lichen *Cladonia*, and the blue-green, filamentous *Nostoc* in *Peltigera*. Although each individual Lichen is of characteristic form, it has been found possible to produce them artificially by sowing the appropriate fungal spores among the cells of the normal algal partner.

Reference to Fig. 365 will give some indication of the internal structure of a typical Lichen. The fungal hyphae covering both upper and lower surfaces are dense and thick-walled, thus providing adequate protection against drought for the internal components. Tufts of hyphae characteristically project from the lower surface into the substratum and function for absorption. In those Lichens which colonise rock-faces penetration is facilitated by the secretion of solvents.

It will be apparent that the Algae benefit from the association by the protection afforded and by the acquisition of a source of water-supply, even in times of drought. The internal spaces amongst the fungal hyphae permit gaseous diffusion, so that carbon dioxide is available for photosynthesis, part of the products of which may, in return, be absorbed by the Fungus.

The normal method of reproduction of this dual organism is interest-

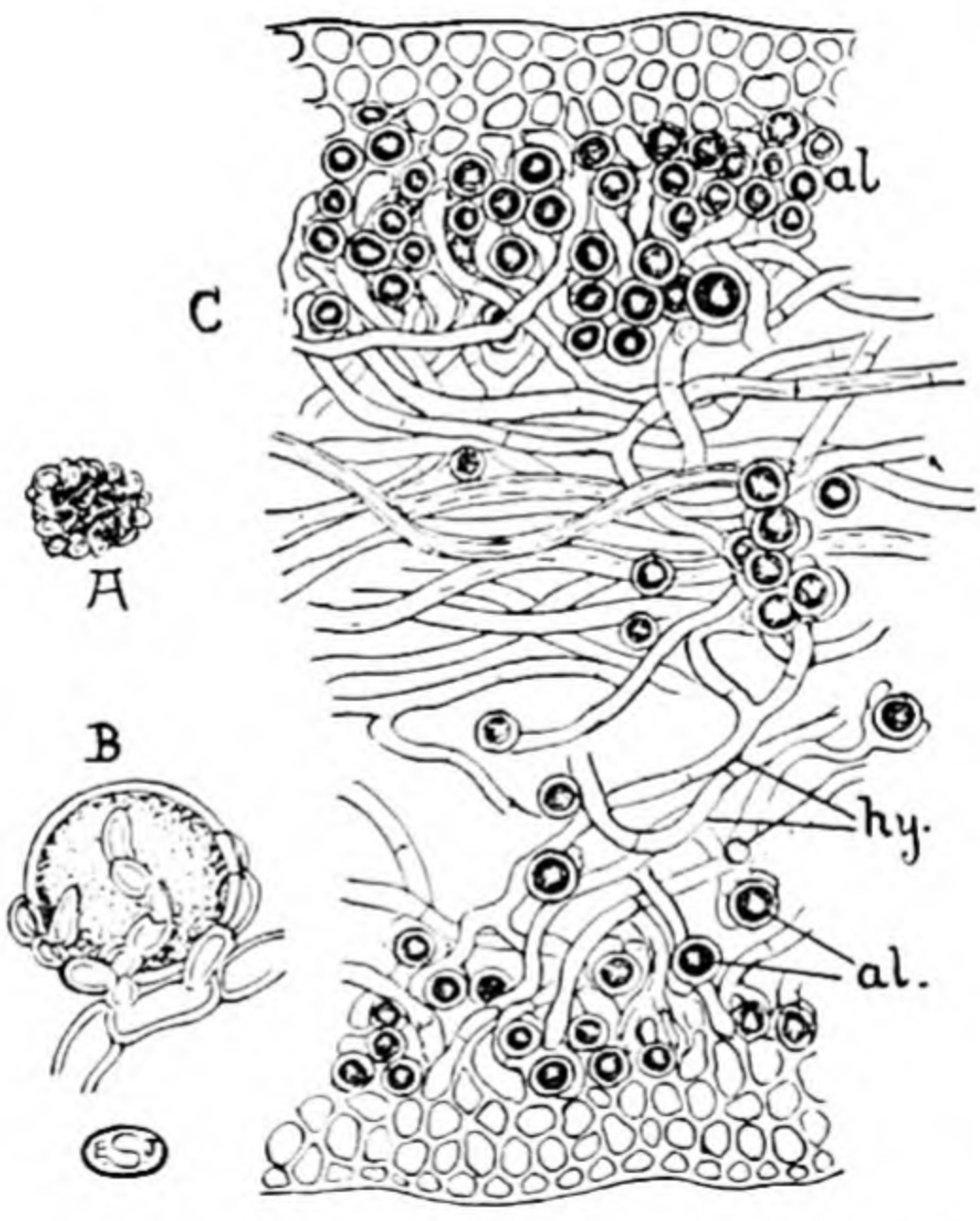


FIG. 365 – *A.*, Soredium, and *C.*, section through the thallus, of the Lichen *Xanthoria parietina*. *al.*, algal cells; *hy.*, fungal hyphae. *B.*, An algal cell from the Lichen *Cladonia*, illustrating the intimate relationship between it and the fungal hyphae. (*B.*, After Bornet.) (From *Plant Form and Function*, by F. E. Fritsch and E. J. Salisbury. Bell.)

ing. Fragmentation occurs to such an extent that the Lichen assumes a powdery appearance. Each fragment consists of a few interlacing hyphae, enclosing algal cells, and the granules, termed **soredia**, are distributed by wind, so that propagation is often rapid.

Mycorrhiza

Almost all underground absorbing systems operate in conjunction with soil Fungi, collectively termed **Mycorrhiza**. In general such association may be regarded as one of symbiosis. The benefits derived by each partner vary, as do the methods by which they are imparted. The reader is referred to *Mycorrhiza*, by J. L. Harley (School Science Review, Vol. XXXIII, No. 119) for a very full account of this phenomenon, and here an attempt will be made to present some of the more general features of the information contained in that article.

The adult host plant may derive benefit through one or more of several possible contributions by the Fungus, which may (*a*) fix atmospheric nitrogen, or (*b*) conduct materials from soil to root-tissues, involving intimate connexion between Fungus and host. Such benefit may result from the mere increase in absorptive area over and above that provided by the root-hairs, or it may be due to digestive activities on the part of the Fungus, rendering certain soil-substances suitable for absorption by the host. (*c*) Within the root-tissues the Fungus may assist in the elaboration of enzymes or vitamins, syntheses which the host cannot perform unaided. The Fungus may, on the other hand, be operative only in the seedling stage, possibly stimulating germination.

The Fungus may benefit from the association (*a*) by obtaining a ready supply of carbohydrates and amino-acids direct from the host plant; (*b*) it may obtain bios (page 376) from the host plant, or (*c*) it may find the internal environment of the root tissues more suitable than that of the surrounding soil.

Much work has been performed on the Orchidaceae in connexion with symbiosis. Here it has been discovered that only in very special conditions will seeds germinate in the absence of the appropriate Fungus. Such stimulation may be due to the provision of organic materials or to the neutralisation of dormancy-promoting substances in the testa. The seeds are originally Fungus-free – i.e., there is no transmission from parent to offspring – and only the underground parts must become infected if successful growth is to take place. Every new branch root becomes separately infected.

The fungal hyphae actually penetrate the epidermis of the subterranean organs of the host and coil within the cortical cells. In this region they retain their form, but deeper in the cortex they become disintegrated as a result of digestive activity by the host plant. The whole mycelium is therefore in intimate contact with host tissues at the one end and with soil particles at the other.

Mycorrhiza has also been investigated in other groups. The families Leguminosae and Gramineae amongst Angiosperms, some Gymnosperms and even Liverworts are associated with non-septate Fungi, which penetrate the host cells, forming large oil-filled *vesicles*, and in some cases brush-like *arbuscules*, rather reminiscent of haustoria. This particular Fungus is *Rhizophagus*. In these cases, however, no adverse effects appear in the host if fungal infection is prevented.

Members of the family Ericaceae grow mainly on soils rich in raw humus, and here it might well be imagined that the supply of available compounds of nitrogen is low. Dr M. C. Rayner diagnosed the Fungus entering into association with the roots of at least some members of this family as a species of *Phoma*. The hyphae make intimate contact with the root-tissues and may even penetrate aerial portions of healthy plants, and the seed-coats in addition. The Fungus presumably converts the complex nitrogen compounds of the raw humus into a form suitable for absorption by the host roots. Indeed they may also assist in such absorption, and in addition may be capable of the fixation of atmospheric nitrogen. The Fungus also appeared necessary for successful germination.

The Mycorrhiza so far considered are all described as *endotrophic*, indicating that they penetrate the organs with which they are associated and form an *internal* connexion. In some families, however, notably the Pinaceae and the Cupuliferae, the Mycorrhiza are *ectotrophic*, forming a sheath around the roots and penetrating only the superficial layers of the cortex. The hyphae here combine to form a network, known as the *Hartig net*, possibly with some intracellular penetration. It is probable in this case that the Fungus benefits the host by increasing the absorptive area in contact with the soil.

The growth of Mycorrhiza in general seems to be encouraged by deficiencies of certain mineral elements in the soil, notably potassium, phosphorus, nitrogen and possibly calcium. In these conditions there may well be excess sugars in the roots, since syntheses beyond that resulting in the formation of sugars will thereby be restricted. The fact that Mycorrhiza require simple sugars when grown in culture would appear to substantiate this view.

Thus, in general, symbiosis may be regarded evolutionarily as the highest grade of association between organisms, for the adaptation of the partners, each to the other, shows that essential requirement for success in the perpetual struggle for existence.

APPENDIX I

As well as the usual laboratory reagents and apparatus, the following materials should be kept in stock. Except where instructions are given, it is recommended that the reagents be purchased already in solution. Further guidance in the making up of reagents may be obtained by the consultation of such standard works as Peacock's 'Elementary Micro-technique'.

Aceto-carmine.
Alcohol (30%, 50%, 70%, 90% and absolute).
An auxanometer.
Benedict's Solution. 8.6 gms. of crystalline copper sulphate, 86 gms. of sodium citrate and 50 gms. of anhydrous sodium carbonate in 500 c.c. of water.
Borax Carmine (70% alcohol).
Bouin's Fluid.
Canada Balsam.
Ehrlich's Haematoxylin (aqueous).
Eosin (aqueous).
Fehling's Solution. *a*. 35 gms. of crystalline copper sulphate in 500 c.c. of water.

b. 60 gms. of sodium hydroxide and 173 gms. of sodium potassium tartrate in 500 c.c. of water.

When required add to *a* sufficient of *b* just to re-dissolve the precipitate of copper hydroxide which is first formed.
Gelatin.
Giemsa Stain (methylene-blue-eosin).
Glucose.
Glycerol.
Haematoxylin (aqueous).
Iodine Solution in alcohol.
Iodine Solution in benzene.
Iron Alum.
Iron Haematoxylin.
Klinostat.
Leishmann's Stain.
Light Green.
Mercuric-acetic solution. Add one volume of glacial acetic acid to nine of saturated mercuric chloride solution.

Methylene-blue (aqueous).

Millon's Reagent. Make up a 10% solution (by volume) of sulphuric acid, and dissolve in it 10 gms. of mercuric sulphate for every 100 c.c. of dilute acid (by grinding successive small quantities of the solid with the acid in a large mortar). Then add to every 100 c.c. of the solution 10 c.c. of a 1% solution of sodium nitrite in water. The solution keeps quite well, but if the solutions of mercuric sulphate and sodium nitrite are stored separately and mixed only as required, it will keep indefinitely.

α-naphthol (2% alcoholic solution).

Paracarmine.

Paraffin Wax (Melting-point about 50° C.).

Phloroglucin (alcoholic).

Safranin (50% alcoholic solution).

Schultz's Solution (chlor-zinc-iodide) (aqueous).

Sucrose.

Tannic Acid.

Thymol (3% alcoholic solution).

Tidman's Sea Salt. (A 2% solution gives an osmotic pressure of 15.9 atmospheres and other concentrations proportionate values, providing that moderate dilutions are employed.)

Xylene.

APPENDIX II

THE RAT

It is intended here to deal briefly with the biology of the rat in so far as it differs from that of the rabbit, already fully described in Chapter 8. A knowledge of the latter will be assumed, so that only important points of difference, suitably illustrated, will be detailed.

Together with such other animals as mice, guinea pigs, squirrels, voles and beavers, the rat belongs to the order of mammals known as the **Rodentia**, characterised by the habit of gnawing their food, for which purpose they are equipped with large, chisel-shaped incisor teeth. The rat is very widely distributed and there are two common species. The colour of the fur of the tropical rat (*Rattus rattus*) is very dark brown or black, whilst that of the northern rat (*Rattus norvegicus*) is a lighter brown. The latter is also larger. The laboratory rat is an albino form bred from *R. norvegicus* and is widely used for experimental purposes.

External Characters

The vibrissae, of tactile function, are divisible into a number of groups – the *mystacial* (behind the nose), the *submental* (on the lower jaw), the *superciliary* (over each eye), the *inter-ramal* (on the chin) and,

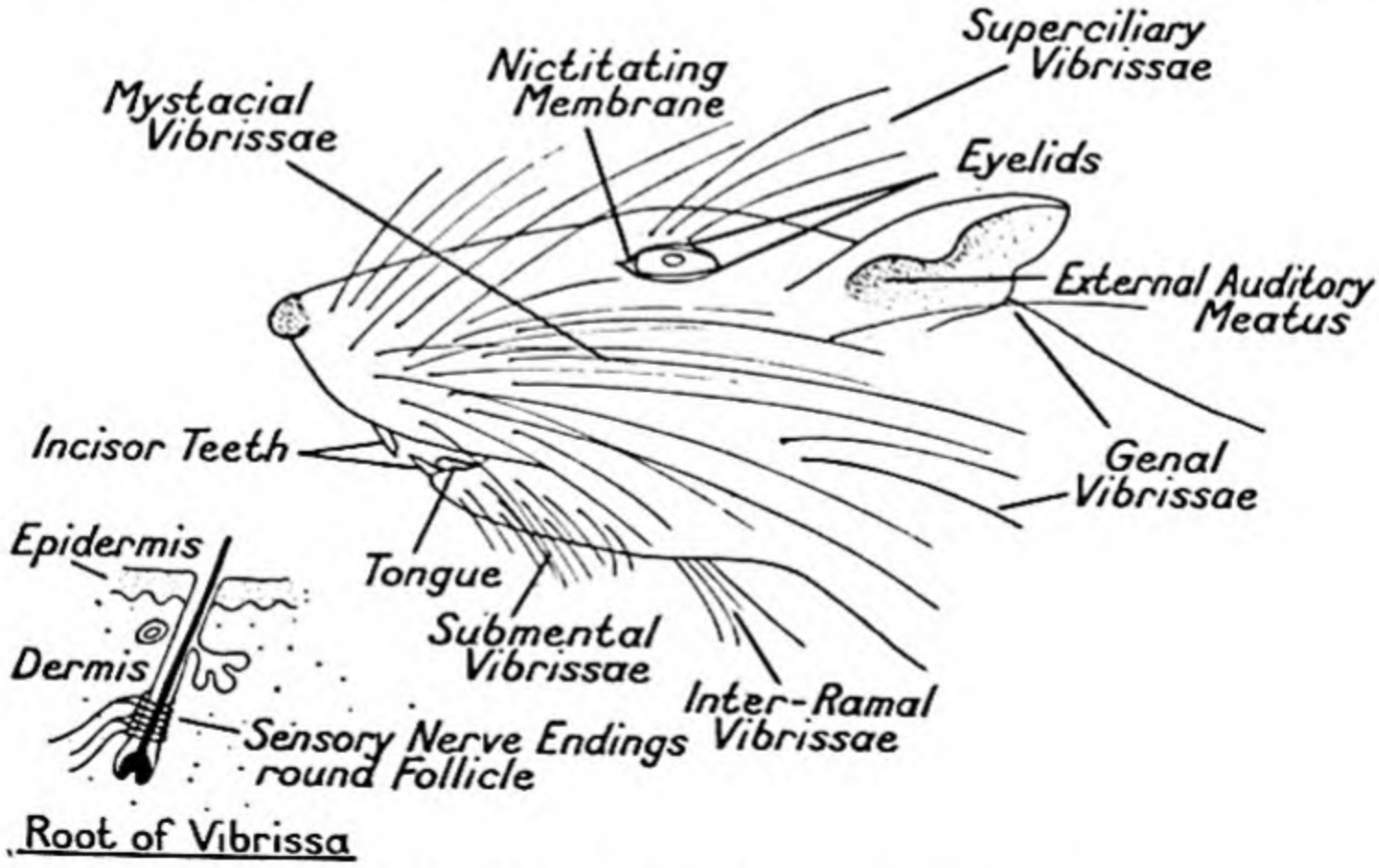


FIG. 366 – External features of the head of the rat, in lateral view. (From *The Rat*, by T. A. G. Wells. Heinemann.)

rather sparsely, the *genal* (on each cheek). A functional nictitating membrane (page 139) is present in the anterior corner of each eye. Compared with those of the rabbit, the pinnae are small and their associated muscles weak. There are normally six pairs of nipples, distributed over almost the entire length of the trunk. The tail is very long and is largely used as a balancing organ. It bears rings of overlapping scales, from between which short hairs emerge. The feet are naked and on each fore foot only four digits are apparent, the thumb being vestigial and represented only by a small swelling and flattened claw.

Skeleton

Here the only point of note is the numbers of vertebrae in the respective regions of the vertebral column. These are – cervical 7 (as in the rabbit), thoracic 13 (12 in the rabbit), lumbar 6 (7 in the rabbit), sacral 2 (usually 1 in the rabbit) and caudal 26–30 (about 18 in the rabbit).

Alimentary System

The dental formula of the rat is:

$$\frac{1003}{1003} \text{ Total} = 16$$

Folds of skin extend from the cheeks deeply into each diastema (page 152). Although the rat is essentially herbivorous, to which habit its dentition is suitably adapted, it also consumes dead plant and animal matter. Rats living wild near human habitations eat domestic waste and stored food.

On either side of the head there are three salivary glands, termed respectively the *sublingual*, the *submaxillary* and the *parotid*. The last-named characteristically possesses a very long duct, known as *Stenson's duct*. Lymph nodes are embedded in all the salivary glands. There are two pairs of lachrymal glands – the *intra-orbital* (beneath each eye) and the *exorbital* (beneath each ear). In addition, there is a *Harderian gland* around each optic nerve: its oily secretion is discharged on to the nictitating membrane. Behind each parotid gland is a mass of adipose (fatty) tissue, sometimes termed the *hibernating gland*, though its function is obscure. Reference to Fig. 367 will make clear the relative positions of these various glands.

The liver is deeply cleft into four lobes, termed respectively *right*, *left*, *median* (or *cystic*) and *caudate* (or *Spigelian*) lobes. There being no gall bladder, the ducts from these lobes unite to discharge bile directly into the duodenum through an aperture surrounded by a sphincter muscle. The pancreas is drained by a series of ducts, opening separately into the conjoined bile duct. Bearing in mind the relative sizes of the rabbit and the rat, the caecum of the latter is proportionately much smaller, whilst

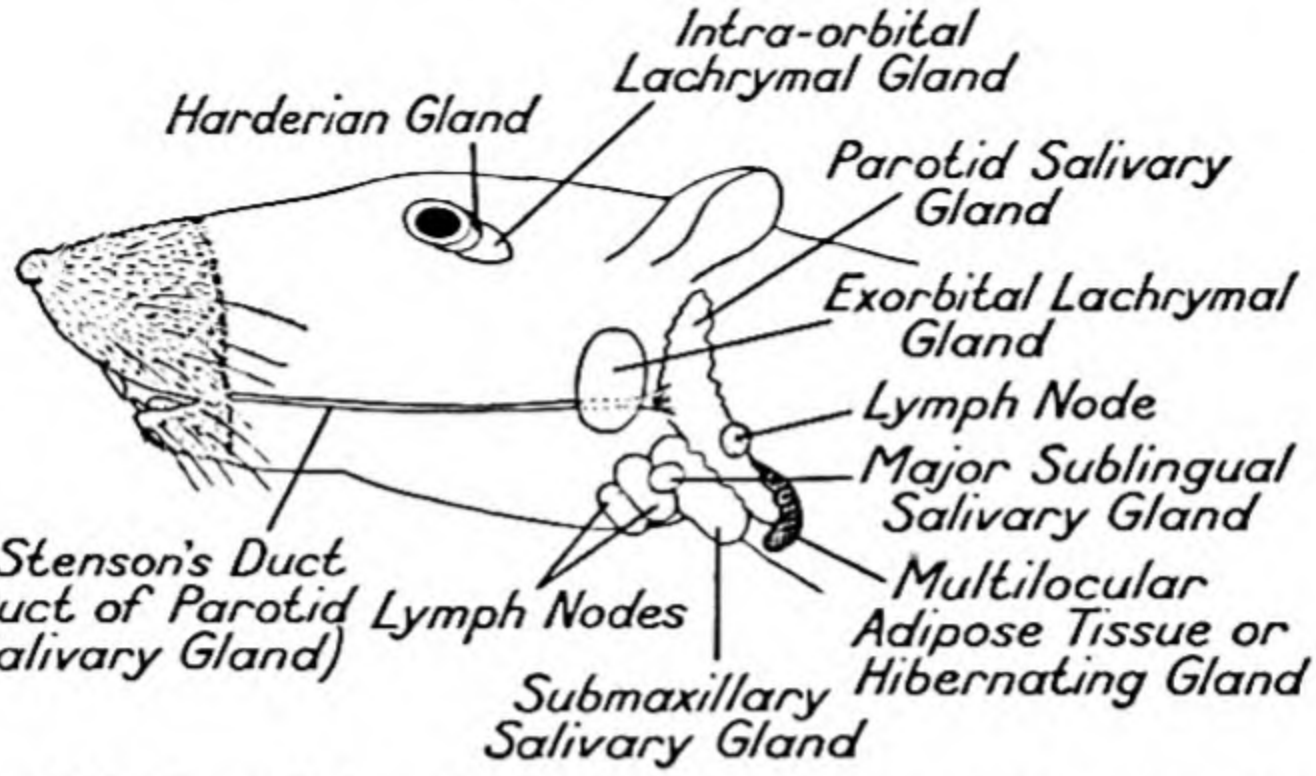


FIG. 367 – Lateral view of the head of the rat, with the skin removed. (From *The Rat*, by T. A. G. Wells. Heinemann.)

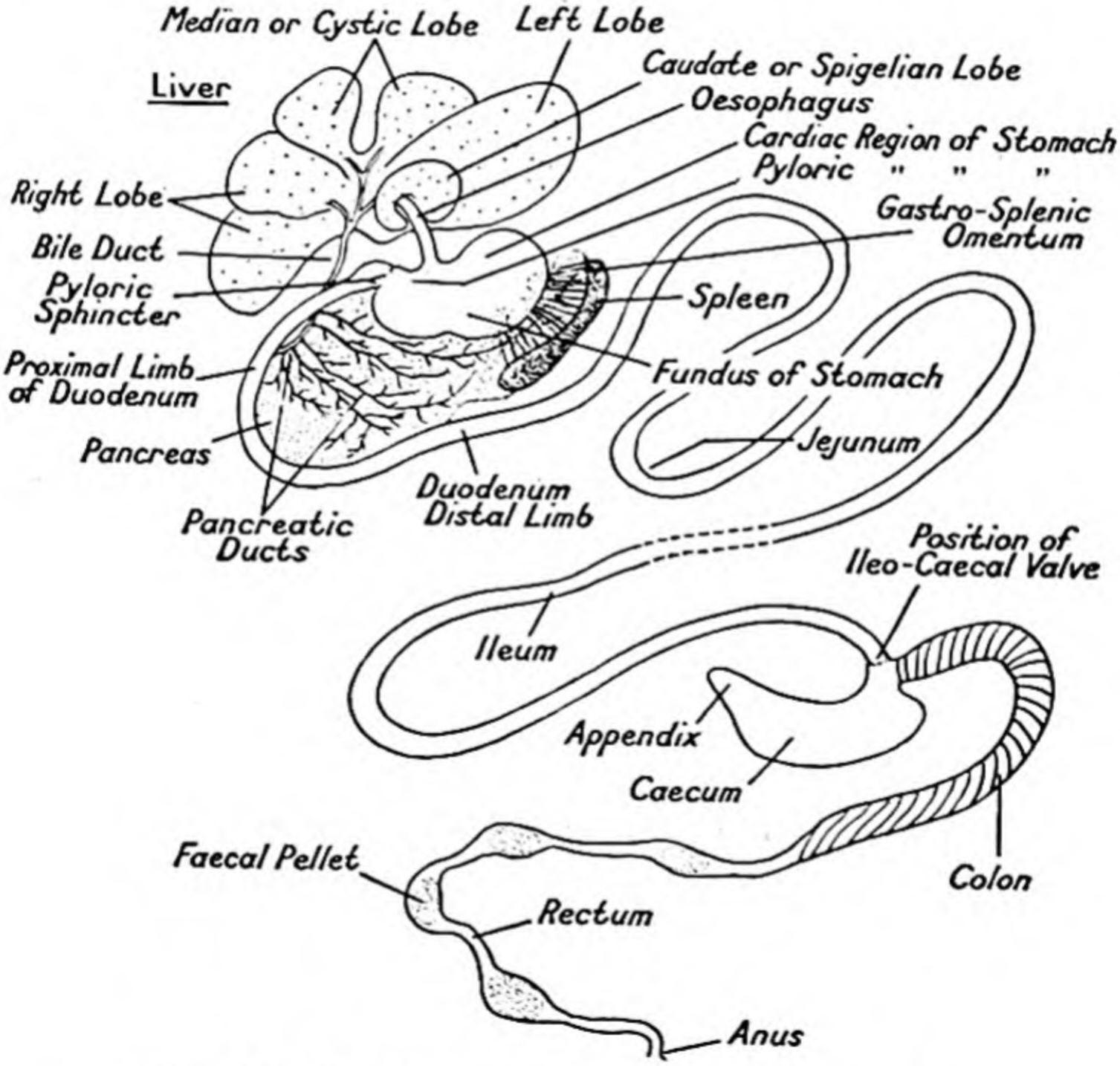


FIG. 368 – The alimentary canal of the rat displayed. (From *The Rat*, by T. A. G. Wells. Heinemann.)

the appendix is less clearly demarcated. The general form of the alimentary canal of the rat is shown in Fig. 368.

Urino-genital System

In the male rat there are a few peculiarities of note, mainly involving the accessory glands concerned with sperm nutrition and ejaculation. The seminal vesicles take the form of rubbery, curved, leaf-like masses, fixed to the base of the urethra. On the concave side of every mass is a

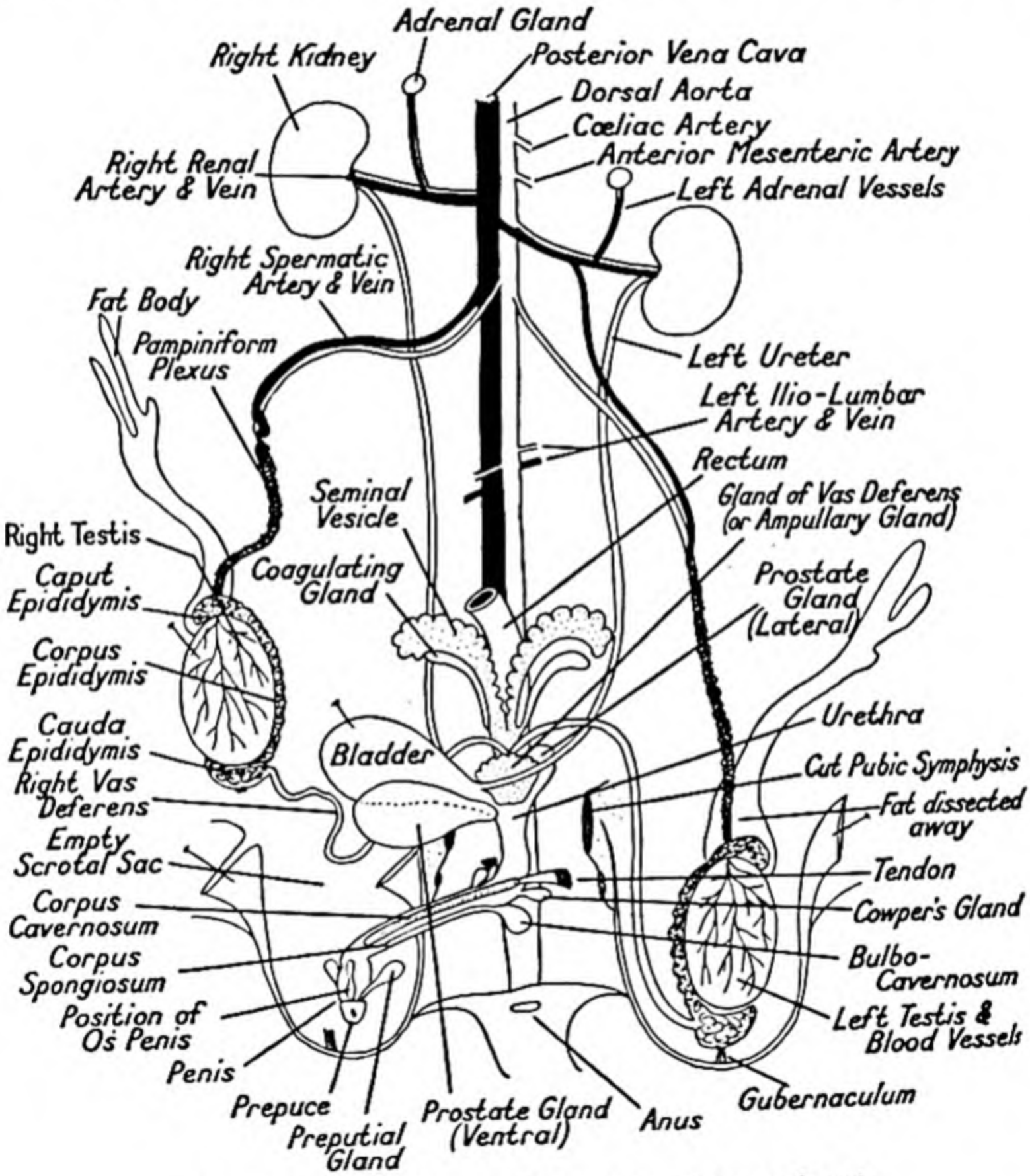


FIG. 369–The urino-genital system of the male rat.
(From *The Rat*, by T. A. G. Wells. Heinemann.)

coagulating gland. Surrounding the two vasa deferentia, where they converge upon the neck of the bladder, is an *ampullary gland*. The prostates take the form of a large ventral lobe, together with a smaller

lobe on either side of the neck of the bladder; their secretion is responsible for the activation of spermatozoa. Where the urethra is free there is a pair of Cowper's glands. A pair of *preputial glands* is loosely attached to the penis, very close to the tip. Internally, the penis contains a very small bone – the *os penis* – adding support to the penis during copulation. As indicated on page 349, erection is primarily achieved by increased blood-pressure in the spongy tissue of the penis. The structure of the male urino-genital system is indicated in Fig. 369.

INDEX

Where several references to a word are given, the most significant is shown in heavy type. Page-references to illustrations are denoted by the addition of a letter 'F'.

ABDOMEN, 71
Abdominal pore, 82
Abscission layer, 261
Absorption, by animals, 393–4
  by plants, 376–80, 382–3
Accommodation, 169
Acetabulum, 118, **145**
Acetyl choline, 468, 487
Achene, 283
Acquired characters, inheritance of, 616
Acromegaly, 482
Acromion process, 116, 144
Acrosome, function of, 562
Actinomorphic, 265, 267, 270
Adaptation, 621–24
  embryonic, 623
  in plants, 623–4
  in Vertebrata, 619–20
  physiological, 622
Adipose tissue, 323
Adrenal body, 138, 176
  hormones of, 468 **485–6**
Adrenalin, 406, 468, **484–5**
Adsorption, 308, 383
Adventitious roots, 228, 258, **289**
Aerial shoots, 238–9F
Afferent, *see* 'Artery' *and* 'Nerve-fibre'
'After-birth', 563
Agaricus, 209F–10
  nutrition of, 408
  practical work, 214
Agglutination, 327
Agranuloctyes,358
Air-bladder, 598
Albinism, 433
Albumen, 73, 108
Albumen sac, 536
Albuminous cells, of leaf of *Pinus*, 233
Alchemilla, 560
Alcohol, preparation of, 439–40
Aleurone grains, 407
Algae, 3, 5, 181 *et seq.*
Alimentary canal, development of in *Branchiostoma*, 505–6
  in *Rana*, 521
Alimentary system, of *Lumbricus*, 55F, 56
  of *Oryctolagus*, 151–6
  of *Periplaneta*, 72F–3
  of *Rana*, 120–2F
  of *Scyliorhinus*, 89–90, 92F
Alkaloids, 449, 451
Allantoic placenta, 543F
Allantois, 536, 543, 544, 623
Allelomorphs, 572, 581–2
Alternation of generations, 557–9
  evolutionary significance of, 600
  in animals, 559–60
  in plants, 557–9
Alveolus, of lung, 157F, 330, 424
  of pancreas, 345F
  of tooth, 155
Amaryllidaceae, 634F–5
Amino-acids, 343, 344, **371**, 391, 400, 403, 447
Amitosis, 311
Ammonia, 400, 445, 447
Amnio-cardiac vesicle, 536
Amnion, development of, in *Gallus*, 533–5F
  in *Oryctolagus*, 542–3
Amoeba, 3F–8
  practical work, 23–4
Amphicoelous, 87
Amphioxus, *see* '*Branchiostoma*'
Ampulla, 104, 134
  of Lorenzini, 103
Amygdalin, 407, 449

Amylase, 73, 390, 391, 392
Anabolism, 369, 417
Analogous organs, 596
Anapophysis, 143
Anatomy, comparative, as evidence for evolution, 594–9
Androecium, 265
Androgens, 487
Anemophilous, 277
Angiospermae, 238 *et seq.*, 258
  leaf, 253–61F
  root, 288–98F
  stem, 238–40F
Annelida, 44, 52, **64**, 65, 66, 129
Annual, 290
  rings of Angiospermae, 249
  rings of *Pinus*, 231
Annulus, of *Agaricus*, 209
  of sporangium of *Dryopteris*, 225, 226
  of sporogonium of *Funaria*, 221
Anopheles, 18
Antenna, 69–70
Anterior fontanelle, 86, 87
Anterior vena cava, of *Orcytolagus*, 161
  of *Rana*, 127–8, 522
Anther, 268
Antheridial cell, 235
Antheridium, of *Dryopteris*, 228F
  of *Fucus*, 196
  of *Funaria*, 221F
  of *Pellia*, 216–17F
  of *Pythium*, 202
  of *Volvox*, 187
Anthocyanin, 449, 450
Anthozoa, 560
Anti-bodies, 328, 357
Antigens, 328, 357
Antipodal cells, 277
Anti-toxins, 210
Anus, 52, 71, 73, 110, 139, 156, 327, 599
Aorta, of *Oryctolagus*, 158–9
Apocarpous, 268
Apogamy, 561
Apophysis, 222
Appendages, 67, 69, 81
Appendix, 156
Aqueduct of Sylvius, 99, 131, 162
Aqueous humour, 167
Archaeornis, 592F–93
Archegonium, of *Dryopteris*, 228F
  of *Funaria*, 221F
  of *Pellia*, 217–18F
  of *Pinus*, 236
Archenteron, 502, 503, 504
Archesporium, 218, 222, 226, 235 275
Archiform muscles, 64
Archipallium, 472
Area, opaca, 527
  pellucida, 527, 532
  vasculosa, 531
Areolar tissue, 322
Arterial system, evolutionary development of, 609, 610F, 611
Arterial system, of *Oryctolagus*, 158–61, 159F
  of *Rana*, 126–7, 524F
  of *Scyliorhinus*, 92F, 94–6
Artery, 121, **340**
Arthropoda, 65, 67, 81
Artiodactyl, 476
Arytenoid cartilage, 130, 151, 157
Ascaris, 438
Ascogonium, 206
Ascomycetes, 205
Ascospores, 206, 208
Ascus, 206, 208
Assimilation, 394–5
Association neurone, 462, 463
Asymmetrical (flower), 267
Atlas, 116, 142
Atriopore, 507
Atrium, 505, 506–7
Attachment-constriction, 314
Auditory capsule, of *Oryctolagus*, 151
  of *Rana*, 113–14, 132, 134–5
  of *Scyliorhinus*, 87, 105
Auditory strings, 172
Auerbach's plexus, 340
Auricle, 93, 123, 608
Autonomic nervous system, 133–4, 165–6, **466–8F**
Autosomes, **582**, 624
Autostylic jaw-attachment, 116
Autumn coloration, 449
Auxanometer, 418F, 421, 493
Auxins, 417, 493–5
Avoiding reaction, 453
Axil, of leaf, 242
Axis, 143
Axolotl, 561
Axon, 336, 463–4, 473
Azotobacter, 411
Azygospore, of *Mucor*, 205

Bacillus, 211
  mesentericus, 215
  radicicola, *see* '*Rhizobium*'
  subtilis, 215

Bacteria, 8, 53, **210–13**, 410 *et seq.*, 648, 664, 670
and disease, 212–13
and symbiosis, 390
practical work, 215
Bacteriophages, 214
Balanced solutions, 306
Balantidium coli, 21
Bark, 251
Basal granule, 9–10
Basidia, 210
Basidiomycetes, 209
Basidiospores, 210
Basidorsal cartilage, 86
Basihyal cartilage, 88
Basilar membrane, 172
Basiventral cartilage, 86
Basophils, 328
Bast, *see* 'Secondary phloem'
Beggiatoa, 409, 413
Berry, 282
Bicipital groove, 144
Biennials, 290
Bile, 390–1, 488
Bile-channels, 342
Bile-duct, of *Oryctolagus*, 156
of *Rana*, 121
of *Scyliorhinus*, 90
of sheep, 41
Bilirubin, 327, 391
Biliverdin, 391
Binary fission, 7F–8, 11, 21, 182, 602
Bios, 376, 672
Blastocoel, 32–3, 501, 502, 527
Blastocyst, 530, 531
Blastoderm, 527
Blastomere, 501, 508
Blastopore, 502, 511, 528–9
Blastostyle, **34–5**, 365
Blastula, of *Branchiostoma*, 500F
of *Hydra*, 32–3
of *Obelia*, 37
of *Rana*, 508–9
Blepharoplast, 21, 643
Blind spot, 169
Blood, and disease, **357–8**, 599
circulation of in *Oryctolagus*, 161F
in *Rana*, 128–9F
comparative physiology of, 599-600
functions of, 354 *et seq.*
practical work, 350–1
structure of, 326F–8
Blood-clotting, 356
Blood-corpuscles, 18–19
Blood-groups, 358, 600
inheritance of, 581–82
Blood-vessels, of *Lumbricus*, 57F
Body-temperature, 141, 358–9, 406
Body-wall, of *Fasciola*, 39F
of *Hydra*, 25–9F
of *Lumbricus*, 53–4F
of *Taenia*, 44
Bone, *see* 'Skeleton' and its various components
structure of, 325F–6
table of in skull of *Oryctolagus*, 150
Botulism, 213
Bowman's capsule, 330, **444F**, 519, 539, 613
Brachial plexus, 130
Bract, 258
scale, 234
Bracteole, 258
Brain, centres of, 471–3
function of, 465, 468–73
of *Oryctolagus*, 162–4F
of *Rana*, 130F–2
of *Scyliorhinus*, 98F–9F
Branchial arches, 84, 89
Branching, of root, 294–5
of stem, 242
Branchiostoma, 330, 444, 598, 602
embryology of, 499–507F
execretory organs of, 444
Bronchiole, 157F
Bronchus, 130, 157
Broomrape, *see Orobanche*
Brownian movement, 307
Brunner's glands, 340–1F
Bryophyta, 216
Buccal cavity, of *Lumbricus*, 56
of *Periplaneta*, 70–1, 72
of *Rana*, 120
Bud, 239–41, 256–7F
Budding, 251
Bulb, 240F
Bulbil, 256
Bulbus arteriosus, 608

CAECUM, 156, 392
Calcar, 119
Calcium, blood-content of, 474
function of, 374, 375
oxalate, 450–1
pectate, 304
Calyptrogen, 292–3
Calyx, 265
Cambium, 244, 248, 295, 493
interfascicular, 248
Capacitation, 562
Capillaries, 128, **340**, 354–5, 424
Capillarity, 378

Capitulum, inflorescence, 273F
of rib, 142, 143
Capsule, 281
of Glisson, 342
of sporangium of *Dryopteris*, 226
of sporogonium of *Pellia*, 218
Carbohydrates, 369–71, 554
chemical tests for, 383–6
digestion of, 389
excretion of, 445
storage of, 406 *et seq.*
Carbon, circulation of, 410–11F, 664
Carbon dioxide, amount evolved by germinating seeds, 427F–8, 439
and photosynthesis, 396–9, 405
carriage of by blood, 355–6
effect of on germination, 553
evolution of, by germinating seeds, 439
by plants, 427F
necessity of to plants, 405, 416,422
Carotene, 169, 344, 395
Carotid gland, 126
Carpals, 118, 145
Carpels, 264, 265, 268–9, 281
Carpus, of *Oryctolagus*, 145
of *Rana*, 110, 118
Cartilage, 86
structure of, 324F–5
Cartilage-bone, 113, 141, 548–9
Cartilaginous labyrinth, 104, 114
Casein, 375, 390
Caseinogen, 375, 390
Casparian band, 294
Catkins, 266, 277
Cells, 301–9, 339
differentiation of in *Hydra*, 25–8
multiplication of, 310–11, 312F, 313–15F, 316–20
of Rauber, 541
of Sertoli, 348
typical, of animals, 301–2F, 303–4
of plants, 304–5F, 306
Cell-content, 306–8
Cell-membrane, 304
Cell-sap, 302, 306
Cell-wall, 304–6
of Bacteria, 210
of other plants, 304
Cellular structure of organisms, 353
Cellulose, 304, 316, 371
Cement, 68, 154
Cement gland, 524
Centriole, 303, 314
Centromere, 314
Centrosome, 303, 316
Centrum, 86, 116, 142
Cephalisation, 66
Ceratobranchial cartilage, 88
Ceratohyal cartilage, 88
Cercaria, 42, 43F, 44
Cerci anales, 71
Cerebellum, 99, 131, 164
function of, 466, 471–3
Cerebral cortex, 470, 471, **472–3**
Cerebral ganglia, of *Fasciola*, 40
of *Taenia*, 46–7
Cerebral hemispheres, 130, 162
condition of in Craniata, 472
function of, 472–3
Cerebro-spinal fluid, 99
Cerebrum, 98, 472
Cervical flexure, 536
Cervical ribs, 142
Chaetae, 52, 53F, 54F, 59
Chaetigerous sac, 54
Chalazae, 524
Chemosynthesis, 200, 409, 413
Chemotaxis, 218, 228, 454–5
Chiasmata, 317, 318, 597
Chitin, 68, 76
Chlamydomonas, 181–4
Chlamydospore, 204–5
Chloragogenous tissue,54, 59
Chlorella, 397, 398, 399
Chlorobium, 411, 413
Chlorophyll, 182, 194, 642
extraction of, 415
properties of, 395–6
spectrum of, 395F
Chloroplast, 306
of *Chlamydomonas*, 182
of *Euglena*, 643
of *Haematococcus*, 184
of leaf, 261, 476
structure of, 395–6
of *Pleurococcus*, 185
of *Spirogyra*, 187, 305
Chlorotic, 387
Choleocystokinin, 487
Cholesterol, 390–1
Chondrin, 324, 326
Chondroblasts, 86, 324
Chordae tendineae, 123
Chordata, diagnostic features of, 626–7
differences from higher Invertebrata, 81, 626
similarities to higher Invertebrata, 81, 626
Chorion, 533–4
Chorionic tissue, 483

Choroid coat, 167
Choroid plexus, 99, 131, 164
Chromatids, **313**, 314, 317–18, 577
Chromatin, 348
Chromatium, 411, 413
Chromatophore, 196
Chromomeres, 313
Chromonemata, 313, 577
Chromosomes, 235, 310–11, 313
  composition of, 577–9
Cilia, 9–11, 60
Ciliary body, 167, 169
Ciliary muscle, 167
Circumnutation, 422–3F
Cirrus, 41
Cladodes, 239, 623
Clasper, 82, 108
Classification, 626–36
  of animals, 626–8
  of plants, 630–36
Cleavage, in *Branchiostoma*, 501
  in *Gallus*, 527
  in *Oryctolagus*, 540–1
  in *Rana*, 508–9
Climbing plants, 653–6
Clitellum, 53, 63, 64
Clitoris, 175
Cloaca, 82, 90, 105, 108, 110, 121, 135
Clostridium, 410
  botulinum, 213
  pasteureanum, 411
Cnemial crest, 146
Coccidium schubergi, 604
Coccus, 211
Coccyx, 597
Cochlea, 134, 172
Coelenterata, 25, 39, 64–5
Coelenteron, 25, 34
Coelom, 39, 52, 54–5, 97
  development of, 505, 521, 543
  functions of, 64–5
  of *Lumbricus*, 52, 62, 65
  of *Periplaneta*, 73
  of *Scyliorhinus*, 97, 109
Coelomoduct, 443
Coelomostome, 518, **613**, 615
Coenobium, 186F
Coenocyte, 201, 309
Coenosarc, 34
Coleoptile, 457, 553
  in experiments on plant hormones, 490–91
Collagen, 322
Collenchyma, 321F–2
Colleterial glands, 78, 79
Colloid, 307, 308
Colon, of *Oryctolagus*, 156
  of *Periplaneta*, 73
Colony, of cells, 352–3
  of organisms, 359–60
Coloration in animals, 622–23
Colour-blindness, inheritance of, 582–3
Columella, of ear, 115, 135, 172
  of *Funaria*, 222
  of *Mucor*, 204
Columnae carnae, 124–5
Commensalism, 665–6
Companion cell, 231, 338F, 339
Compositae, 258, 266, 633F, **634–5**
Conceptacles, of *Fucus*, 193, 197–8
Conduction of impulses, **459–63**, 470, 494
Cones, of *Pinus*, 233F, 234
Conglobate gland, 79
Conidium, of *Penicillium*, 206
  of *Pythium*, 201
Coniferae, 230
Conjugation, in *Paramecium*, 12–13, 563
  in *Spirogyra*, 188–9
Conjugation canal, 188
Conjunctiva, 169, 544
Connective, 268
Connective tissue, 111, **322F**
Contraction, 26
Conus arteriosus, 93, 124, 608
Convoluta, symbiotic Algae of, 670
Co-ordination, 36
Copromonas, 604
Coraco-branchial muscles, 92F
Coraco-hyoid muscles, 92F
Coracoid cartilage, 88F, 89
Coracoid fontanelle, 117
Coracoid process, 144
Corbiculum, 361
Cork, 231, **241**, 251, 261
Cork cambium, 231, 251, 296
Corm, 240F–1
Cornea, 76, 141, 167
Corolla, 265, 268, 270
Corpora cardiaca, 490
Corpora cavernosa, 349
Corpora quadrigemina, 163, 471
Corpus, of stem apex, 246
Corpus allatum, 490
Corpus callosum, 163
Corpus luteum, 176, 347, 483
  hormones of, 488
Corpus spongiosum, 349
Corpus striatum, function of, 472
Correlation centres, 472–3

Cortex, of adrenal body, 138, 484
of brain, 470
of egg, 516
of *Fucus*, 194
of *Paramecium*, 9
of root, 225, 290
of stem, 243
Cortin, 484
Corymb, 273F
Cotyledons, of Angiospermae, 258, 280–1F
of *Pinus*, 236
Cowper's gland, 175
Cranial flexure, 536
Cranial nerves, 468–70
of *Oryctolagus*, 164–5, 173
of *Rana*, 131–2
of *Scyliorhinus*, 100F, 101–3
Craniata, 81, 354, **626**
Cranium, 84F, **87**, 148
Crayfish, excretory organs of, 443
Creeping stems, 240
Cretinism, 480
Cricoid cartilage, 130, 151, 156
Cristae, 105, 303
Crop, of *Lumbricus*, 56
of *Periplaneta*, 73
Cross-fertilisation, 41, 63
Cross-pollination, 277, 278–9
Crossing-over, 576–8
Cruciferae, 631F–2
Crura cerebri, 99, 131, 163,
Crypts of Lieberkühn, 332 341F
Crystalline cone, 78
Crystalloids, 307, 308, 407
Cucurbita, stem of, 245F
Cultures, 213
Cuscuta, 655F–66F
Cuticle, of *Fasciola*, 39
of hair, 141
of insects, 68F
of leaf, 260
of *Pellia*, 216
of *Taenia*, 45–6
Cutin, 305, 329
Cutis, 503
Cuttings, 258
Cycads, 592, 602–603
Cymose, 242F, 273, 274F
Cyst, 15, 19, 42
Cysticercus, 48, 51
Cystolith, 330–1F
Cytase, 552
Cytochrome, 382, 433, 434
Cytology, 299
Cytopharynx, 9
Cytoplasm, 7–8, 12–13, 18, 19, 182 187, 301
Cytoplasmic inheritance, 588–590
Cytostome, 9, 11, 21

DAFFODIL, *see Narcissus*
Dandelion, 284, 632F
pollination of, 279, 286
Darwin, 617, 624
Decidua, 540
Defaecation, 441–2
Dehydrogenase, 422–3
Delphinium, 267, 270
Deltoid ridge, 144
Dendrites, 335
Denitrification, 412
Dental formula, 152–3
Dental groove, 154
Dental lamina, 155
Denticles, 82, 84
development of, 82–3
Dentine, 83, 120, 154–5
Dependent differentiation, 515
Dermatogen, 246, 280
Dermis, 83, 113, 140
Dermotrichia, 84, 89
Desmogen strands, 248
Detoxication, 328, 344
Development, of Angiosperm, 280–1F
See also Embryology
Diabetes, 485
Diageotropic, 456
Diaphototropic, 457, 623
Diaphragm, 155, 156
of *Funaria* capsule, 222
Diarch root, 225
Diastase, 554
Diastema, 152
Dichasium, 274F
Dichotomy, 193, 216
Dicotyledons, 242, 254, 258
See also Stem, Root *and* Flower
Diencephalon, 98, 163
Differences, between animals and plants, 640 *et seq.*
between living and non-living matter, xii *et seq.*
Differentiation, 192, 195–6, 353–4, 544
of stains, 301–2, 328
Digestion, 389–90
in mammals, 391–2
in other animals, 392–3
Digestive juices, 56
table of in mammals, 392
Dihybrid ratio, 574–5

Diploblastica, 65
Diplococci, 211
Diploid chromosome-number, 313, 314, 497, 557, 558, 560–1
Dipnoi, 614
Disaccharides, 370
Disc florets, 633F
Dispersal of seeds, 283, 284F, 285
Distance receptors, 470
Division of labour, 352 *et seq.*
  in animal communities, 360–4
DNA, 313–14, 348, 394, 578
Dodder, *see Cuscuta*
Dogfish, *see Scyloirhinus*
Dominance, evolution of, 619
  partial, 580–1
Dominant gene, 571–2
Dorsal aorta, 696, 698
  development of in *Rana*, 521
  of *Oryctolagus*, 158
  of *Rana*, 136, 516, 522
  of *Scyliorhinus*, 95
Dorsal pore, 52, 59
Dorsal root, 103, 132, 460, 461, 462–3
Drosophila, 570, 574, 576, 577, 580, 616–17
Drupe, 282F
Dryopteris, 223–9F
  practical work, 229
Ductless glands:
  (Endocrine organs), of *Oryctolagus*, 176
  of *Rana*, 137–8
  of *Scyliorhinus*, 108
Ductus arteriosus, 161, 165, 538, 539, 609
Ductus caroticus, 608
Ductus Cuvieri, 94, 522, 608, 611, 613
Ductus ejaculatorius, 79
Ductus endolymphaticus, 104, 135, 546
Ductus venosus, 538, 539
Duodenum, of *Oryctolagus*, 155–6
  of *Rana*, 121
  of *Scyliorhinus*, 90
Dura mater, 99, 131, 164
Dwarf shoots, 230, 242

EAR, development of, 546–7F
  of *Oryctolagus*, 170–2F
  of *Rana*, 134F–5
  of *Scyliorhinus*, 103–4F
Ear ossicles, 151, 172
  homologies of, 547
Earthworm, *see Lumbricus*
Ecdysis, 68, 79–80
Ectoderm, development of, 502, 527
  of gut of *Periplaneta*, 72
  of *Hydra*, 25, 26F, 27–8F
  of *Lumbricus*, 55
  of *Obelia*, 34–5
Ectodermal cell, of *Fasciola*, 42
Ectoplasm, 3–9, 11, 302, 642
Education, biological significance of, 473
Effector organ, 462
Efferent, *see* Artery *and* Nerve-fibre
Egg, of *Branchiostoma*, 499
  of *Gallus*, 526F
  of *Oryctolagus*, 540
  of *Rana*, 502
  of *Scyliorhinus*, 500F–1
  symmetry of, 500
Egg groove, 63F
Egg sac, 62, 136
Electricity, effect of on growth, 421–2
Electrolytes, 308
Elongation, 244–8, 293–4
  measurement of, 418–19
  region of maximum, 419F
Elytra, 71
Embryo, 48, 524
  of angiosperm, development of, 280–1F
Embryo sac, of Angiospermae, 276, 279–80
  of *Pinus*, 235F
Embryology, as evidence for evolution, 600–1
  See also *Branchiostoma*, *Gallus*, *Oryctolagus* and *Rana*
Embryonic cell, of *Taenia*, 48
Embryonic membranes, of *Gallus*, 532–3F
  of *Oryctolagus*, 543F
Embryonic plate, 541
Embryophore, 48
Emulsion, 307–8
Enamel, 83, 120, 154
Enamel organ, 83, 155
Endocardium, 521, 537
Endocarp, 282
Endochondral, 549
Endocrine organs, 479 *et seq.*
  of *Oryctolagus*, 176
  of *Rana*, 137–8
  of *Scyliorhinus*, 108–9
Endoderm, development of, 502, 527
  of *Hydra*, 25, 26F, 28F, 29
  of *Lumbricus*, 55
  of *Periplaneta*, 72
Endodermis, of leaf of *Pinus*, 233

of root, 225, 290, 294
of stem, 243
Endogenous, 288, 294
Endolymph, 104, 134, 135, 172
Endophragmal skeleton, 79, 81
Endoplasm, 3–11, 302, 642
Endosperm, 533, 534
of Angiospermae, 280
of *Pinus*, 236
Endostyle, 506
homology of, 506, 598
Energid, 308
Energy, xiii, 341, 423, 663–4
conservation of, 369, 664
Entamoebae, 24
Enterokinase, 391
Entomophilous, 277
Environment, 618
adaptation to, xiv, 621–24
and the organism, 638–9
animate, 663–74
as cause of variation, 616 *et seq.*
effect of on evolution, 616 *et seq.*
gradient between organism and, 327
inanimate, 639–62
internal, 479
unusual, 644–5
Enzymes, 7, 204, **389–90**, 554
of digestion, 390–3
of respiration, 432 *et seq.*
Eosinophils, 328
Epiblast, 502, 528
Epiboly, 502
Epibranchial cartilage, 88
Epicalyx, 267F
Epicarp, 282
Epicoracoid cartilage, 117
Epicotyl, 550, 551F(B)
Epidermis, of *Fasciola*, 39
of leaf, 225, 231, 258, 261, 328
of *Lumbricus*, 53, 61
of *Pinus*, 231
of skin, 83, 113, 140
of sporogonium of *Funaria*, 222
of stem, 243
Epididymis, 174, 330, 347, 614
Epigeal germination, 237, 550–1F
Epiglottis, 157
Epigynous, 266F, 286
Epipetalous, 267
Epiphytes, 666
Epipleur, 507
Episternum, 117
Epithelium, 329
coelomic, 53–5, 62, 138
structure of, 329F–30
Epithem, 381
Epoöphoron, 615
Erepsin, 391
Ergosterol, 372, 390
Erythroblasts, 327
Erythrocytes, 326, 327, 344
Etiolation, **421**, 476, 492
Eudorina, 352–3
Euglena, 642–3F
affinities of, 644
nutrition of, 644
Eustachian canal, 150
Eustachian tube, 81, 121, 135, 157
development of in *Rana*, 519
homology of, 601
Evolution, 285–6, 591
evidence for, 591–625
mechanism of, 616–25
modern, 605
of vertebrate urino-genital system, 613–15
of vertebrate vascular system, 607–13
Excretion, 65, 134, **441**
chemistry of, 445–7
Excretory organs, 442–5
of Chordata, 444–5
Excretory pores, of *Fasciola*, 39
of insects, 76
Excretory system, of *Lumbricus*, 59–60
Exocrine glands, 332
Exodermis, 294
Exogenous, 248, 288
Exoskeleton, 67, 76, 79, 81
Expiration, of *Oryctolagus*, 423
of *Periplaneta*, 75
of *Rana*, 425
of *Scyliorhinus*, 91
External auditory meatus, 150
External characters, of *Fasciola*, 39
of *Lumbricus*, 52–3F
of *Oryctolagus*, 139–41
of *Periplaneta*, 68–71
of *Rana*, 110–11
of *Scyliorhinus*, 81, 82F, 83
of *Taenia*, 44
External form, of animals and plants compared, 640–1
Extine, 275
Extra-branchial cartilage, 89
Eye, of Arthropoda, 69, 77F
of Vertebrata, 166–70
development of, 544, 545F, 546
Eye-lid, 110, 141

Eye-muscles, 101, 132, 543

FAECES, 73, 110, 327
Falciform ligament, 90, 97, 151
False palate, 151, 592
Fasciola, 39–44F, 51
Fats, 73, 371–2
  chemical tests for, 356
  digestion of, 391–2
  excretion of, 445–6
  formation of in plants, 401
  storage of, 406
Fat body, of *Periplaneta*, 73, 76
Female cones, of *Pinus*, 235F–6
Femur, of *Oryctolagus*, 145–6F
  of *Periplaneta*, 71
  of *Rana*, 118
Fenestra ovalis, 114, 135, 151
Fermentation, 435, 438
  by yeast, 208, 439
Fertilisation, 310 *et seq.*, 562–3
  in Angiospermae, 379–80
  in *Branchiostoma*, 499–501
  in birds, 497, 562
  in *Dryopteris*, 228
  in *Fasciola*, 41–2
  in fish, 562
  in *Fucus*, 197
  in *Gallus*, 526–7
  in *Hydra*, 31–3
  in *Lumbricus*, 63–4
  in Mammalia, 562–3
  in *Obelia*, 36–7
  in *Oryctolagus*, 540
  in *Pellia*, 218
  in *Periplaneta*, 79
  in *Pinus*, 234–6
  in *Rana*, 137, 562
  in *Scyliorhinus*, 108, 562
  in *Taenia*, 48
  mechanism of, 499–501
Fertilisin, 499
Fibres, of Angiospermae, 322–3
  of *Fucus*, 194
Fibrin, 357
Fibrinogen, 327, 344, 357
Filament, 268
File, 246
Fin, 82, 89, 480
Fin-rays, 89
Flagellum, 21, 182, 217, 643
Flame-cell, 40F, 46, 442, 444, 507
Flank meristem, 246
Flavones, 449
Flight, of insects, 474
Flocculus, 163
Floral diagram, 264
  of buttercup, 264F
  of daffodil, 635F
  of primrose, 278F
  of sweet pea, 272F
  of *Viola*, 631F
  of wild hyacinth, 634F
  of wild rose, 631F
Floral formula, 265
Flower, 264–87
  evolution of, 285–6
  modifications of, 266–8
  practical work, 286–7
  For individual flowers see pages listed under 'Floral diagram' *and also pages* 631–36
Foetus, 561
Food, absorption of, by animals, 393–4
  by plants, 256, 376–82
  of *Amoeba*, 3–6
  of animals, 369–75
  of *Fasciola*, 39
  of *Lumbricus*, 56
  of *Paramecium*, 11
  of *Periplaneta*, 67
  of plants, 375–6
  of *Rana*, 120
  of *Taenia*, 46
Foramen, 87, 115, 131, 142, 164
Foramina, of skull of dog, 149–51
  table of, 150
Fore-limb, of Cetacea and Sirenia, 597
  of *Oryctolagus*, 143–4
  of *Rana*, 116–18
Formative cell, 53, 54F
Fossils, 590–93
Fovea centralis, 169
'Free martin', 489
Fringe, 168
Frond, of *Dryopteris*, 225
  of *Fucus*, 192
Fructose, 370, 393
Fruit, 281
  classification of, 281, 282F, 283
  practical work, 287
Fucoxanthin, 194
Fucus, 192–8, 353, 354
  practical work, 198, 366
Funaria, 220–3
  practical work, 229
Fungi, 200 *et seq.*

GALACTOSE, 370, 391
Gall-bladder, of *Oryctolagus*, 156

of *Rana*, 121
of *Scyliorhinus*, 90
Gallus, embryology of, 526–39
Gametangia, of *Mucor*, 204
Gametes, differentiation of, 15, 17
of *Chlamydomonas*, 183
of *Fucus*, 196
of *Plasmodium*, 18–19
Gametocyst, 14, 15F, 18
Gametocyte, 14, 17, 18, 20
Gametogenesis, 318–20
Gametophyte, 216, 218–19, 223, 228, 236, **557**
Gamont, of *Plasmodium*, 18
Gamopetalous, 268
Ganglion, 60, 76
anterior cervical autonomic, 165, **467**
collateral, 467
dorsal root, 132, 460, **463**
Gasserian, 101, 132, 134
geniculate, 132
lateral, 467
mesenteric, 165–6
petrosal, 132
posterior cervical autonomic, 165, **467**
stellate, 461
vagus, 102, 165
Gaseous exchange, 7, 58, 111, **424–5**
Gastric juice, 390
Gastrula, 502
Gastrulation, in *Branchiostoma*, 501–502
in *Gallus*, 527–9
in *Rana*, 510–11, 516
Gel, 5, 307
Gelatin, 326
Gemmation, 208
Gene, 569, *et seq.*
Gene-complex, 579, 584, 618, 624, 620–21
selection of, 620
Generative nucleus, 279
Genes, complementary, 580–81
Genital atrium, of *Fasciola*, 41
of *Taenia*, 48
Genital pore, of *Fasciola*, 39
Genital pouch, 71, 79
Genome, 579, 620
Genotype, 573–5, 623
Geographical distribution, 603–4
Geotropism, 455–7
explanation of, 491
Germ-cells, maturation of, 318–20
Germ-layers, 502, 541–42
Germination, 550–52F
changes accompanying, 554
conditions regulating, 553
epigeal, 550, 551F
hypogeal, 550, 551F
of Monocotyledons, 551F, 552F–8
of *Pinus* seed, 236
practical work, 554–5
Gestation, 176, 563
Geum, 276F
Giant cells, 61
Gibberellins, 494
Gills, external, of *Rana*, 519, 522–3F, 524
of *Agaricus*, 209
of *Scyliorhinus*, 90–2
Gill-plate, 209, 252
Gill-rays, 89
Gill-slits, 81, 82, 89, 90, 601
development of, in *Branchiostoma*, 505–6
in *Gallus*, 538
in *Rana*, 519, 522
Girdle, pectoral, of *Oryctolagus*, 143–4F
of *Rana*, 116, 117F, 118
of *Scyliorhinus*, 88F, 89
Girdle, pelvic, of *Oryctolagus*, 143–4F
of *Rana*, 116, 117F, 118
of *Scyliorhinus*, 88F, 89
Gizzard, of *Lumbricus*, 56
of *Periplaneta*, 73
Gland, 121, 330
Gland-cells, 46, 330–1F
Glenoid cavity, 89, 117, 144
Glomerulus, 444, 445, 447, 613
of olfactory bulb, 173
Glossina morsitans, 21, 23
Glossina palpalis, 21, 23
Glottis, 121, 129
Glucose, 327, 370, 391, 406, 407, 445
Glucoside, 407, 449
Glutinants, 28
Glycerol, 372, 401
Glycogen, 11, 73, 162, 208, 343, **370–1**, 406, 485
Gnathostomata, 598, 601, 607 *et seq*
Goitre, 481
Golgi material, 303–4
Gonads, and their ducts, formation of, 519, 614
development of, in *Branchiostoma*, 505
hormones of, in birds, 488
in mammals, 487–8
Gonapophyses, 71, 79

Gonocoel, 505
Gonotheca, 35
Graafian follicle, 175, 176, 346F, 488, 540
Grafting, 257–8
Grana, 395–6F
Granulocytes, 328
Grey crescent, 501, 508
Grey matter, 99, 131, 463–4
Growing point, of *Fucus*, 194
  of root of Angiospermae, 292–4
  of root of *Pinus*, 231
  of stem, 245–8
Growth, 417–23
  conditions regulating, 420–1
  effect of phyone on, 482
  grand period of, 420
  in animals, 423
  measurement of in plants, 418F, 419F, 420
Guard-cells, 233, 243, 259F–61, 404–5
Gubernaculum, 174
Gullet, of *Euglena*, 643
  of medusa, 35
  of *Paramecium*, 9, 10F
Gymnospermae, 230, 630
Gynaecium, 268–9

HAEMAL ARCH, 87
Haemamoeba, see Plasmodium
Haematococcus, 184
Haemocoel, 65, 71, 73, 442
Haemoglobin, 17–18, 58, 327, 581
  and respiration, 434
Hair, 139
Hair-follicle, 140
Hallux, 119–20
Haploid chromosome-number, 313, 499, 557, 558, 560–1
Hatschek's nephridium, 507
Hatschek's pit, 505
Haustoria, 658
Haversian canal, 154, 326, 549
Head, of *Nereis*, 65F
  of *Periplaneta*, 68F–71
Head-cavities, of *Branchiostoma*, 505
Head-fold, development of, 529, 583–4
Heart, development of, in *Rana*, 521
  evolutionary development of, 607–8
  of Chordata, 81
  of *Oryctolagus*, 157–81
  of *Periplaneta*, 73–4
  of *Rana*, 113, 114F, 115–16
  of *Scyliorhinus*, 93F, 97
Heart-wood, 404
Heat, evolution of by germinating seeds, 439
Helianthus, stem of, 243F
Helicotrema, 172
Hemicellulose, 304
Hepatic caeca, 73, 393
Hepaticae, 216
Heredity and evolution, 567 *et seq.*
Hermaphrodite, 40–1, 47–8, 62, 63, 290, 561
Heterodont dentition, 151
Heterogamy, 556
Heteromita, 604
Heterostyly, 279, 588
Heterothallism, 205, 586
Heterozygous, 572, 581
Hexacanth, 46, 48
Hilum, 406–7
Hind-limb, of *Oryctolagus*, 145–6F
  of *Rana*, 118–20
Hippuris, 649F
Histology, 299
Hold-fast, 192
Holoblastic cleavage, 501
Holophytic nutrition, 408
Holozoic nutrition, 408
Homologous chromosomes, 313, 317, 571, 572
Homology, of organs, 596–7
Homozygous, 572
Honey bee, division of labour, 360F, 361F, 362F, 363
Hormones, 344, 479–95
  of animals, 480–89
  of plants, 490–95
Horse, fossil pedigree of, 593
Host, 13, 44
  intermediate, 20, 23, 42–3, 50
Humus, 646
Hydathodes, 381F–2
Hydatid cyst, 51
Hydra, 25–33, 559–60
  differentiation in, 354
  practical work, 37–8, 366
  symbiotic Algae of, 669
Hydranths, 34–6
Hydrocaulus, 34–5
Hydrochloric acid, 390
Hydrogen ion, 374
  effect of, on guard-cells, 405
    on respiration and heart-beat, 374
Hydrolysis, 374, 389, 393
  of disaccharides, 370
  of fats, 371

of polysaccharides, 371
of proteins, 371
Hydrophytes, 650–52
Hydrorhiza, 34
Hydrotheca, 35
Hydrotropism, 458–9
Hymenial layer, 210
Hyoid, of *Oryctolagus*, 151
of *Rana*, 115, 425
Hyoid arch, 84, 88
Hyomandibula, 88, 116, 547
Hyostylic jaw-attachment, 89
Hypha, of *Agaricus*, 209
of *Mucor*, 203, 408
of *Pythium*, 200
Hypoblast, 502, 528
Hypobranchial cartilage, 87
Hypocotyl, structure of, 297F
Hypodermis, 233
Hypogynous, 266F, 286
Hypopharynx, 70F
Hypophysis, 98, 108, 130, 163, 481
homology of, 598
Hypostome, 25, 34

ILEUM, of *Periplaneta*, 73
of *Scyliorhinus*, 90
Imago, 69
Immunisation, 357–8
Implantation, 540
Individuality, 364–5
Indusium, 226
Inferior (gynaecium), 266
Inflorescence, 267, 273–4
cymose, 274F
racemose, 273F
Infundibulum, 98, 108, 130, 163, **481**
Ingestion, 5F
Inheritance, mechanism of, 569–90
Inner cell-mass, 540
Inoculation, 358
Insecta, 67
Inspiration, of *Oryctolagus*, 423–4
of *Rana*, 425
of *Scyliorhinus*, 91
Instar, 80, 489
Insulin, 406, 407, 483–4, **486**
Integument, 235, 277, 557
Interdorsal cartilage, 86
Intermediate forms, evolutionary significance of, 602–3
Internode, 238
Inter-renal body, 109, 138
Interstitial cells, 26–8F, 354
Intestine, of *Lumbricus*, 56
of *Oryctolagus*, 155–6
of *Rana*, 121, 393F
of *Scyliorhinus*, 89–90
structure of wall of, 340–1F
Intine, 275
Inversion of retina, 543–4F
Invertebrata, 66, 129
comparison with Chordata, 81, 626
Involucre, 218, 258
Iodine, 373, 374, 480–1
Ions, effect of various, in animals, 373
in plants, 375
Iris, 167, 169
Iron, valency of, in cytochrome, 434
in haemoglobin, 434
Irritability, xiv, 51, 30–1, 453, 473
Island faunas, 601
Islets of Langerhans, 109, 176, 345F, 486
Isogamy, 556
Isotonic, 307
Isotopes, radio-active, 399

JAW, attachment of, 88–9, 115
lower, in *Oryctolagus*, 151
in *Rana*, 115–16
in *Scyliorhinus*, 88–9
upper, in *Oryctolagus*, 151
in *Rana*, 115–16
in *Scyliorhinus*, 88–9

KAPPA PARTICLES, 588
Katabolism, 369, 419
Keel, 271
Kidney, development of, in chordate prototype, 512–13
in *Gallus*, 539
in *Rana*, 518–19F
of Chordata, 443F, 444F–5
of *Oryctolagus*, 174, 176
of *Rana*, 135, 615
of *Scyliorhinus*, 105, 614
Kinetin, kinins, 495
Klinostat, 455–6
Kölliker's pit, 503

LABIUM, 70, 362F
Labrum, 70–1
Lacinia, 70
Lactase, 391–2
Lacteal, 393
Lactic acid, 445
Lactose, 370, 374, 391
Lagena, 105
Lamarck, 616
Lamina, 253

Larva, 37, 562
of *Fasciola*, 42
of insects, 80, 564
of *Rana*, 522, 564
Larynx, of *Oryctolagus*, 156
of *Rana*, 121, 130, 521
Lasso, 29F
Latent period, 466
Lateral line, 83, 102
Lateral plate, 517
Lathroea, 668
Laurer-stieda canal, 41–2
Leaf, external structure, 253F–60
internal structure, 258, 259F, 260, 261F
of *Dryopteris*, 224F, 225
of *Pinus*, 231, 232F, 233
types of, 258
Leaf-fall, 261–2F, 449
Leaf-trace, 248
Leaves, arrangement of, 254
modifications of, 255–6
Lecithin, 343, 390
Legume, 271, 282F
Leguminosae, 271, 277–8, 411
see also Sweet pea
pollination in, 277–9
Lens, 167, 542
Lenticel, 238
formation of, 251, 296
Leucocytes, 58, 75, 327
Leucoplasts, 215, 406
Lichens, 669F–70
Life-history, 555 *et seq.*
as evidence for evolution, 600–602
of Angiospermae, 274–80
of animals and plants, 556–65
of Bacteria, 211–12
of *Fasciola*, 42, 43F, 44
of *Funaria*, 223
of *Hydra*, 31–2, 37
of *Lumbricus*, 623
of *Monocystis*, 14, 15F, 16–17
of moths and butterflies, 79–80, 563
of *Mucor*, 204–5
of parasites, 564–5
of *Pellia*, 219, 223
of *Penicillium*, 206
of *Pinus*, 234–6
of Pteridophyta, 223
of *Pythium*, 202
of *Taenia*, 48, 49F, 50–1
specialised types of, 564–5
Light, effect of, on growth and elongation, 420–1
on guard-cells, 404–5
on position of chloroplasts, 476
necessity of for photosynthesis, 397
see also Photoperiodism *and* Phototropism
Lignin, 305
Ligula, 362F
Liliaceae, 634F, 635
Limnaea truncatula, 42
Linkage, 575–6
Lipase, 73, 391
Liver, functions of, **343–5**, 406, 445, 447
of *Oryctolagus*, 156
of *Rana*, 121, 128
of *Scyliorhinus*, 90, 96
structure of, 341–3F
Liverwort, *see Pellia*
Lobi inferiores, 98
Locomotion, in *Amoeba*, 4
in *Chlamydomonas*, 182
in *Hydra*, 30, 36
in *Lumbricus*, 57–8
in *Paramecium*, 10
in *Volvox*, 186F
Locomotory organs, 474–6
Lumbricus, 52–66F
practical work, 66
Lungs, of *Oryctolagus*, 156, 157F
of *Rana*, 126, 128, 129
Lyginopteris, 593
Lymph, 129, 355
Lymph-hearts, 129
Lymph-sacs, 111, 129
Lymph-vessels, 129, 162
Lymphatic system, of *Oryctolagus*, 162
of *Rana*, 129
Lymphocytes, 328
Lysis, 541
Lysosomes, 303

MACERATION, 350
Macrophage, 323
Magnoliaceae, 265
Maize, germination of, 552F-3
Male nuclei, of pollen grain, 235, 279
Malic acid, 228, 454
Malaria, 17
control of, 22–3
Malpighian corpuscle, 444, 519, 613
Malpighian tubules, 73, 442, 444, 445
Maltase, 73, 391, 392
Maltose, 370, 390
Mammalia, 141

evolutionary development of, 598 *et seq.*
Mammary glands, 141, 176
Mandible, of *Periplaneta*, 70
Mandibular arch, 84, 87–8
Mantle, 426
Manubrium, 35, 36
Marrow-cavity, 325F–6
Matrix, 322, 324
Maxilla, of *Periplaneta*, 70
Meckel's cartilage, 88–9, 115
Medulla, of adrenal body, 138, 485
of brain, 99, 131
of *Fucus*, 194
of hair, 140
Medullary rays, of *Pinus*, 231
of root, 296
of stem, 248–9, 250
Medullary sheath *see* Myelin sheath
of vascular bundle, 244
Medusa, 35–6F, 569–70
Megakaryocytes, 228
Megasporangium, of *Pinus*, 234, 235
Megaspore, of Angiospermae, 276
of *Pinus*, 235
Megaspore mother-cell, 275–6F
Megasporophyll, 234, 236
Meibomian glands, 141
Meiosis, 198, 235, **318–20**, 508, 511, 574
Meissner's plexus, 340
Melanin, 168, 508
Membrane-bone, 113, 141, 549
Membranous labyrinth, 104, 114
Mendel, Gregor Johann, 569 *et seq.*
Mendel's laws, 569–70
Meningeal membranes, 164
Meristematic tissue, 244, 245
'Mermaid's purse', 108
Meroblastic cleavage, 527
Merogony, 18
Meront, of *Plasmodium*, 18
Merozoite, of *Plasmodium*, 18
Mesencephalon, 98, 131, 163–4
Mesenchyme, 46, 324, 518
Mesenteron, 72, 73
Mesentery, 519
Mesethmoid cartilage, 87
Mesocardia, 537
Mesocarp, 282
Mesoderm, 52, 64, 502
development of, 504–5, 511, 530–32, 542
Mesogloea, 25, 28
Mesonephros, 105, 108, 537, **613–14**
condition of in newt, 614
development of in *Rana*, 518–19
homologies of, 615
Mesophyll, 225, 260
Mesophyte, 258
Metabolism, 369, 403–4, 417
Metacarpals, 118, 145
Metacarpus, 110
Metachronal rhythm, 10
Metamorphosis, 561, 564
in insects, 80, 564
in *Rana*, 523, 525
effect of thyroxin on, 481
Metanephrogenous tissue, 539
Metanephros, 105, 614–15
origin of, 539, 613
Metapleur, 506–7
Metapophysis, 143
Metatarsus, 110
Metaxylem, of root, 291, 294
of stem, 244
Metazoa, 3, 50
Metencephalon, 98–9, 131, 163
Micropyle, 235, 236, 277, 550
Microsomes, 305, 577
Microsporangium, of *Pinus*, 234
Microspore, of *Pinus*, 234
Microspore mother-cell, 275
Microsporophyll, 234
Middle lamella, 196, 304, 316
Milk, 374–5
Mimicry, 622–23
Mimosa, sensitivity of, 492
Mineral salts, as plant food, 375–6, 382–3
concentration of in blood, 372
in animal diet, 372–4
Miracidium larva, 42, 43F, 44
Mitochondria, 303–4
Mitosis, 311–16, 500, 562
differences in animal and plant cells, 316
Mitral cell, 173
Mollusca, 426
excretory organs of, 443
Monochasium, 274F
Monocotyledons, 242, 250F, 254, 258, 291–2
Monocystis, 13–17
practical work, 24
Monocytes, 328
Monohybrid ratio, 570–1
Monopodium, 242F
Monosaccharides, 370
Morula, of *Oryctolagus*, 540
of *Taenia*, 48

Mosquito, 18, 19, 23
Moss, *see Funaria*
Motility, in animals and plants compared, 640
Motorium, 11
Mouth, of *Fasciola*, 39
of *Hydra*, 25
of *Lumbricus*, 52
of *Oryctolagus*, 151–3, 155
of *Periplaneta*, 70
of *Rana*, 120
of *Scyliorhinus*, 82
Movement, in animals and plants, 474–7
Mucilage, 305
Mucor, 203–5
nutrition of, 408, 657
practical work, 214
Mucous membrane, 425
Müllerian duct, 613
condition of in Gnathostomata, 614, 615, 616
development of, in *Rana*, 519
in *Gallus*, 539
of *Rana*, 135
of *Scyliorhinus*, 106, 107
Multiple fission, 15
Musci, 216
Muscles, effect of pituitrin on, 484
of *Fasciola*, 39
of *Lumbricus*, 53–4F, 59
of *Taenia*, 46
structure of, 333, 334F, 335F
Muscular tone, 476
Musculo-epithelial cells, 26–8F, 340, 354, 360, 485
Mushroom, *see Agaricus*
Mushroom-shaped gland, 78
Mutations, 619, 620, 621
as basis for evolution, 618–19
Mycelium, 200, 203, 205, 210
Mycorrhiza, 672–4
Myelencephalon, 98, 131, 134, 164
Myelin sheath, 336
Myocardium, 521, 537
Myocoel, 505
Myocyte, 14
Myofibrillae, 303, 333, 334
Myomere, 503, 518
Myoneme, 9F, 11
Myxoedema, 481

Narcissus, 266, 632F
Nasal capsule, of *Oryctolagus*, 148
of Rana, 113–14
of *Scyliorhinus*, 87
Nasal organs, of *Rana*, 134
Natural selection, 617, 623
Neck, of archegonium, 217, 221, 236
Nectar-guides, 268
Nectary, 268, 270F, 362
Nematoblast, 26F, 27–8F, 354
Nematocil, 27, 29
Nematocyst, 27, 29
Neopallium, 472
Nephridia, of *Branchiostoma*, 504
of *Lumbricus*, 52, 55, 59F, 60
Nephridiopores, 52, 60
Nephrocoel, 518, 613
Nephrodium, *see Dryopteris*
Nephrostome, 59F, 60
Nephrotome, 105, 518, 531, 613
Nerve, *see* Nervous system
Nerve-cells, of *Hydra*, 28F, 29, 354
of *Lumbricus*, 61
structure of, 335, 336F, 337
Nerve-cord, 65, 81, 86
of *Lumbricus*, 60
of *Periplaneta*, 76
origin of in vertebrates, 502–3F, 511–12, 529, 542
Nerve-fibres, 61
Nerve-nets, 60, 61
Nerve-rings, of medusa, 36
Nervous system, of *Lumbricus*, 60–1
of *Oryctolagus*, 162–6
of *Periplaneta*, 76
of *Rana*, 130–3
of *Scyliorhinus*, 97–105
Neural arch, 86, 116, 142
Neural canal, 511
Neural crest, 513, 529
Neural fold, 502, 511, 529, 542
Neural plate, 501, 502, 511
Neural spine, 116, 142
Neurenteric canal, 503, 505, 513
Neurilemma, 336
Neurocranium, 86F, 87, 113
Neurofibrillae, 336
Neuroglial cells, 169, 337
Neuromast system, 103
Neuronemes, 10–11
Neuropore, 503, 511
Neurula, 511, 513F, 514F
Neutrophils, 378
Nictitating membrane, 139, 410, 598
Nidation, 540
Nipple, 140
Nissl granules, 303, 335
Nitrates, 400–1, 410F–11F
Nitrites, 400, 410F–11F
Nitrobacter, 409, 412

Nitrogen, circulation of, 411–12, 664
  fixation of, 411–12
Nitrosomonas, 409, 410
Node, of Ranvier, 336
  of stem, 238, 254
Nostril, 82, 105, 114, 156
Notochord, 81, 86, 87
  development of, 501–502, 512F, 504, 511, 542
Nucellus, of ovule, of Angiospermae, 238, 275–6F
  of *Pinus*, 235
Nuclear membrane, 310, 318
Nuclear sap, 310
Nuclear spindle, 314, 317–18
Nucleolus, 301, 310
Nucleoplasm, 301
Nucleus, 3, 7–8, 14, 17–18, 177, 182, 187, **301, 310–11**
  mega-, 9, 12–13
  micro-, 9, 12–13
  migratory, 12, 588
  stationary, 12
Nut, 281
Nutrition, 73, 182, 369–416
  of animals and plants compared, 640
  of Bacteria, 211
  of *Euglena*, 644
  relationship between animals and plants, 408–14, 663 *et seq.*
Nymph, 79–80

Obelia, 33–9
  alternation of generations in, 559-60
  individuality of, 364–5
  practical work, 38
Ocellus, 69
Odontoblasts, 155
Odontoid process, 143
Oesophageal glands, 56
Oesophagus, of *Lumbricus*, 56
  of *Oryctolagus*, 155–6
  of *Periplaneta*, 73
  of *Rana*, 121
  of *Scyliorhinus*, 90
Oestrogen, 482, 486–7, 541
Oidia, of *Mucor*, 205
Oils, 372. *See also* Fats
Olecranon fossa, 145
Olecranon process, 117–18
Olein, 372
Olfactory lobes, 98, 130, 134, 162
Olfactory organs, of *Scyliorhinus*, 98, 100, 105
Omentum, 97
Ommatidia, 76–8
Onchosphere, 48
Ontogeny, 600
Oöcytes, 319, 500
Oögenesis, 319F–20
Oögonia, of *Fucus*, 197
  of *Pythium*, 202
  of vertebrates, 319
  of *Volvox*, 187
Oösphere, of Angiospermae, 277, 279–80
  of *Pythium*, 202
Oöspore, of *Fucus*, 198
  of *Pinus*, 236
  of *Pythium*, 202
Oötype, 41, 48
Opercular spout, 524
Operculum, 524
  of nematoblast, 27
Optic chiasma, 98, 101, 131, 169
Optic lobes, 98, 131–2, 169
Optic organelle, 61
Optic thalami, 98, 130, 163
  function of, 472
Oral hood, 598
Orbit, 87, 113
Organ, 321, 359
  of corti, 172
Organ-systems, 359–60
Organelles, 4
Organisation, 513–15
Organisation centre, 515
Organism and environment, 637
Ornithorhynchus, 602
Orobanche, 668
Oryctolagus, 139–77
  embryology of, 540–49
  practical work, 177, 549
Osmosis, 377–8
Osmo-regulation, 448–9, 481
Osmotic pressure, 213, 306, **378, 379,** 407, 442
Ossification, 548F
Osteoblasts, 549
Osteoclasts, 549
Osteocytes, 325
Ostia, 73
Ostiole, 196
Ostium, 107, 108
Otoliths, 105
Ovary, of Angiospermae, 238, 268
  of *Fasciola*, 41
  of *Hydra*, 25, 26F, 32
  of *Lumbricus*, 62
  of mammals, 346F–7
  of *Obelia*, 37

of *Oryctolagus*, 175
of *Periplaneta*, 78
of *Rana*, 135
of *Scyliorhinus*, 107–8
of *Taenia*, 48
Oviducal gland, 107F, 108
Oviduct, of *Fasciola*, 41
of *Lumbricus*, 53, 62
of *Oryctolagus*, 175
of *Periplaneta*, 78
of *Rana*, 136
of *Scyliorhinus*, 106, 108
of *Taenia*, 48
Oviparous, 176
Ovipositor, 360
Ovule, of Angiospermae, 238, 269
development of, 275, 276F, 277
of *Pinus*, 235
Ovuliferous scale, 234
Oxidase, 433
Oxygen, evolution of by plants, 415
necessity of, to plants, 422
for germination, 553
part played by in respiration, 429
Oxy-haemoglobin, 58, 434
Oxytosin, 484

PACE-MAKER, 161
Paddles, of aquatic animals, 476
Paedogenesis, 44, 552
Palaeontology, 591–94
Palisade layer, of *Fucus*, 193
of leaf, 225, 260
Palmelloid stage, of *Chlamydomonas*, 183
Palmitin, 372
Pancreas, of *Oryctolagus*, 156, 176
structure of, 345F
of *Rana*, 121
of *Scyliorhinus*, 109
Pancreatic duct, 90, 156
Pancreatic juice, 390–1
Pandorina, 352
Panicle, 274
Papilio polytes, trimorphism of, 622
Pappus, 267, 284
Paraglossa, 70F
Paraglycogen, 14
Paramecin, 13
Paramecium, 8–13, 21
behaviour of, 453–4
practical work, 24
Paramylum, 14, 643
Paraphyses, 197, 210, 221
Parasite, characteristics of, 13, 20–2, 42, 50–1, 200, 408–9
Parasitism, 657 *et seq.*
Paraysmpathetic system, 467–8
Parathyrin, 486
Parathyroid gland, 176, 486
Parenchyma, of *Fasciola*, 39–40
of plants, 321
of *Taenia*, 46
Paroöphoron, 614
Parthenogenesis, 44, 560–1, 584–5
in honey bee, 560, 585
Parturition, 176
Passage cell, 292, 294
Pasteurisation, 213
Payer's patches, 156
Peduncle, 273
Pellia, 216–17
practical work, 229
Pellicle, 9, 10F
Pelvis, 145
Penetrants, 27
Penicillium, 205–6
practical work, 214
Penis, of *Fasciola*, 41
of *Oryctolagus*, 139, 176–7
structure of, 359
of *Taenia*, 48
Pentadactyl limb, 596, 622
Pepsin, 341, 390
Peptide, 371, 391
Perennial, 290
Perianth, 238, 268
Periblast, 527
Periblem, 246
Pericardio-peritoneal canal, 97
Pericardium, 73, 93, 97, 123
Pericarp, 280, 624
Perichondrium, 324, 548–9
Pericycle, 225, 233, 243, 294
Periderm, 251, 296
Perigynous, 266F, 286
Perilymph, 104, 134, 135, 172
Perineal gland, 140, 141
Period of incubation, 19
Periosteum, 155, 323, 326, 549
Periplaneta, 67–80
practical work, 80
Perisarc, 35
Perisperm, 280, 559
Perissodactyl, 476
Peristalsis, 65, 340, 392
Peristomium, 52
Peritoneal cavity, 97
Peritoneum, 37, 135, 156, 521
Peritrophic membrane, 73
Peroxidase, 433
Petal, 264, 267–8

Petiole, 253, 260, 261, 492
Phaeoplast, 193
Phagocyte, 328, 523
Phalanges, of *Oryctolagus*, 145
of *Rana*, 118, 119
Pharyngobranchial cartilage, 87
Pharynx, of *Fasciola*, 39
of *Lumbricus*, 56
of *Oryctolagus*, 156
of *Rana*, 121
of *Scyliorhinus*, 90
Phellem, 251, 296
Phelloderm, 251
Phellogen, 231, 241, 296
Phenotype, 570–1
Phloem, of leaf, 233, 260
of root, 225, 291
of stem, 231, 244
function of, 402, 403
primary, 249
secondary, 249
structure of, 337, 338F, 339
Phobotaxis, 453
Photolysis, 398
Photonasty, 476
Photoperiodism, 421, 494
Photoreceptors, of *Lumbricus*, 61
Photosynthesis, 395–9
mechanism of, 396–9
Photosynthetic quotient, 396
Phototaxis, 454
Phototropism, 457–9
explanation of, 489–91
Phycomycetes, 205
Phyllode, 253, 602, 624
Phyllotaxis, 254
Phylogeny, 595–601
Phyone, 482
Physiological incompatibility, 277, 586–8
Physiology, 367
comparative, as evidence for evolution, 598–9
Phytochrome, 495
Pia mater, 99, 131, 164
Pileus, 209
Piliferous layer, 293
Pineal eye, 595
Pineal stalk, 98, 130, 163
Pinna, 139, 225
Pinus, 230–6
dispersal of seeds, 285
practical work, 237
Pistil, 238, 268–9F
Pitcher plant, 256
Pith, 244
Pits, 323F–24
bordered, 337–8F
Pituitary body, 98, 108, 130, 138, 163 176, 478, **481–5**
Pituitrin, 484
Placenta, of carpel, 269F
of *Oryctolagus*, 176, 542, 543F, 544
of sporangium of *Dryopteris*, 225
Placentation, types of, 269F–70
Placoid scales, 83, 84, 120
Planaria, 50
Planula larva, 37
Plasma, 75, 327, 355
Plasma membrane, 306, 384
Plasmalemma, 304, 516
Plasmodium, 16F, 17–20 24, 408
Plasmolysis, 306
Plastid inheritance, 589
Plastids, 194, 306, 396
Plastochron, 247
Plastome, 590
Platelets, 328, 356
Platyhelminthes, 39, 44, 46, 52, 65, 66, 560
Pleodorina, 353
Plerome, 246, 280
Pleura, 71, 173
Pleurococcus, 185
Plumule, of Angiospermae, 280
of *Pinus*, 236
Podical plates, 71
Polar body, 320, 347, 561
Pollen-basket, 361–2F
Pollen-brush, 361–2F
Pollen-grains, of Angiospermae, 275–6
development of, 276F
of *Pinus*, 234F–5
Pollen sacs, of *Pinus*, 234
Pollen tube, 235, 279
Pollex, 118
Pollination, 234–5, 277–9
evolutionary significance of, 600
Polychasium, 274F
Polyembryony, 44
Polymorphism, 560
Polypetalous, 268
Polyploidy, 585–6
Polyps, 33–4
Polysaccharides, 304, 370–1
Pons Varolii, 164
Posterior vena cava, 127, 162, 522, 608
Potometer, 388F
Precoracoid cartilage, 117
Preoral pit, 505

Preservation of food, 213
Presumptive areas, 513–15
Primary endosperm nucleus, 277
Primitive knot, 528
Primitive streak, 528–9, 542
Primordia, development of, 246–7
Primrose, 278F–9
  inheritance in, 589F–90
Primulaceae, 635–6
Proamnion, 530
Proboscis, 362
Procambial strands, 248
Prochromosomes, 311
Proctodaeum, 72, 79, 332
Proglottides, 44–6, 48, 66
Prolactin, 483
Pronation, 145
Pronephric duct, 105, 518, 613
Pronephros, development of in *Rana*, 613
Propagation, vegetative, 240
  by aerial shoots, 239F–40
  by subterranean shoots, 240F, 241F
Propagative cell, of *Fasciola*, 42, 44
Prophylls, 258
Proprioception, 61, 465–6
Proscolex, 48–9
Prostate gland, 175
Prostomium, 52, 61, 65
Protandrous, 277
Proteins, 344, 371
  digestion of, 390 *et seq.*
  excretion of, 444, 446–7
  storage of in plants, 407
  synthesis of in plants, 246, 400–1
  tests for, 385–6
Prothallus, of Angiospermae, 277
  of *Dryopteris*, 227
  of *Pinus*, 235, 237
Prothrombase, 356
Protococcus, *see Pleurococcus*
Protoderm, 293
Protogynous, 277
Protonema, 223
Protoplasm, xii, 3, 5, 301, 429
  physical nature of, 307–8
Protoplast, 184, 306
Protoxylem, of root, 291, 294
  of stem, 244
Protozoa, 3, 352
  parasitic, 13–24
Pseudobranch, 91
Pseudo-heart, 57
Pseudonavicella, 15–16, 20
Pseudopodium, 4–6, 17, 453
  mechanism of extension of, 4–5
Pteridophyta, 223, 558
Pteridospermae, 592
Pterygia, 89
Pterygo-quadrate cartilage, 88–9
Ptyalin, *see* Amylase
Pulp-cavity, 83, 120, 153, 154–5
Pulvillus, 71
Pupa, 80, 517–18, **564**
Pyloric sphincter muscle, 90, 156, 390
Pylorus, 121
Pyramidal tract, 465
Pyrenoid, 306
  of *Chalmydomonas*, 182
  of *Euglena*, 643
  of *Haematococcus*, 184
  of *Spirogyra*, 187
Pythium, 200, 201F, 202
  practical work, 214

QUADRATE CARTILAGE, 115

RACEME, 273F
Racemose, 242, 273
Radial canals, 36
Radicle, 236, 280, 550
Ramus communicans, 103, 133, 165, 467
  dorsalis, 103, 133
  ventralis, 103, 133
Rana, 110–38
  classification of, 630
  embryology of, 508–25
Ranunculus, 265F, 270–1F
Raphides, 451
Rat, 679–81
Ray florets, 633F
Recapitulation hypothesis, 600–1
Receptacle, 264, 266F
Receptor organ, 461
Recessive gene, 571, 572
Rectal gland, 90
Rectum, of *Oryctolagus*, 156
  of *Periplaneta*, 73
  of *Rana*, 121
  of *Scyliorhinus*, 90
Redia, 42, 43F, 44
Reduction of chromosome-number, 318, 557, 560
Refection, 670
Reflex action, 461–3
Reflex arc, 461–3, 464
Regeneration, 31, 64
Reissner's membrane, 172
Relationships, between animals and plants, 663 *et seq.*
Rennin, 375, 390

Reproduction, xiv, 7, 556–7
asexual, 31, 44, 183, 186–7, 188, 190, 202, **556–7**, 560
of animals and plants compared, 642–4
of *Oryctolagus*, 175–6
of *Rana*, 135–7
sexual, 12, 36–7, 187, **556–7**, 560
see also 'Life-history'
Reproductive system, of *Lumbricus*, 62–4
of *Periplaneta*, 78–9
Reptilia, condition of heart in, 608–9
Resin ducts, 231, 233
Respiration, xiii, 6, 423–38
anaerobic, 435–8
chemistry of, 429–35
external, 424
in animals and plants compared, 423, 641–2
in Chordata, 81
in fish, 425
in *Lumbricus*, 58, 425
in *Oryctolagus*, 423–4
in *Periplaneta*, 75–6
in plants, 426–9
in *Rana*, 425
in *Scyliorhinus*, 81, 90–3, 425
internal, 425
rate of in life-cycle of plant, 429
Respiratory index, 429
system, of *Oryctolagus*, 156–7
of *Periplaneta*, 74–5
of *Rana*, 129–30
of *Scyliorhinus*, 90–3
Response to stimuli, in animals and plants compared, 641
Rete testis, 347
Retina, development of, 545–6F
structure of, 168F–70
Retinula, 77
Rhabdome, 77–8
Rhizobium, 215, 411
Rhizoids, 190, 220, 223
Rhizome, 241F
Rhodopsin, 169–70
Rib meristem, 246–7
Ribs, of *Oryctolagus*, 142, 143
of *Rana*, 116
of *Scyliorhinus*, 87
Ricinus, germination of, 550–1F
Ring canal, 36
RNA, 314, 394, 578
Rods, 168–9
Root, differences from stem, 288
external structure, 288–9
functions of, 289–90, 378
internal structure, 290–4
of Dicotyledon, 291–2F
of Monocotyledon, 292–3F
of Angiospermae, 288–94
of *Dryopteris*, 225
of *Pinus*, 230F–1
origin of lateral members, 294–6
practical work, 298
primary, 288
tap and fibrous, 288–9F
Root-cap, 231, 280, 288–9F, 292
Root-hairs, absorption by, 378, 379
of Angiospermae, 290
of *Dryopteris*, 225
Root-nodules, 46, 411
Root-pressure, 380
Rosaceae, 631F, 633
Rostellum, 45
Rostrum, 87
Runner, 239F–40

SACCHAROMYCES, 205, 206, 207F, 208
Sacci vasculosi, 98
Sacculus, 104, 134
Sacculus rotundus, 156
Sacrum, 143, 145
Saliva, 73, 390, 392–3
Salivary glands, of mammals, 392
of mosquito, 19
of *Periplaneta*, 72, 392
Salivary receptacle, 72
Saprophyte, saprophytic nutrition, 200, 408
Sap-wood, 404
Sarcolemma, 333, 334
Sauropsida, condition of heart in, 608–9
Scalae, of cochlea, 171F, 172
Scale leaves, 241, 256
Scapula, of *Scyliorhinus*, 89
see also Pectoral girdle
Scar, 256
Schizocarpic fruit, 282
Schizogony, 18
Schizont, of *Plasmodium*, 18
Schizozoite, of *Plasmodium*, 18
Sciatic plexus, 133
Sclerenchyma, 323F–4
Sclerotic coat, 113, 166, 545
Sclerotomes, 518
Scolex, 45F, 49F
Scrotal sac, 139, 174
Scyliorhinus, 81–109
practical work, 109

Scyphozoa, 560
Sebaceous gland, 141
Secondary choana, 155
Secondary thickening,
  of root,
    of Dicotyledons, 296F
    of Monocotyledons, 292
  of stem,
    of Dicotyledons, 248, 249F, 260–1
    of Monocotyledons, 250F–1
Secretin, 486
Seed, 563
  formation of, in Angiospermae, 280
    in *Pinus*, 236
  practical work, 287, 554–5
  significance of in life-history, 560
Segmentation, metameric, 65–6, 517
  development of, in *Branchiostoma*, 504, 517
    in *Rana*, 517–18
Selaginella, 558
Self-differentiation, 513, 515
Self-fertilisation, 48
Self-pollination, 277
  avoidance of, 277
Sella turcica, 176
Semi-circular canals, 104, 134
Seminal groove, 53
Seminiferous tubules, 347F, 614
Semi-permeable membrane, 378
Sense organs, of *Lumbricus*, 61
  of *Oryctolagus*, 167–73
  of *Periplaneta*, 76
  of *Rana*, 133–4
  of *Scyliorhinus*, 103–4
Sensillae, 76
Sepals, 238, 264, 267
Serum, 357
Sex, determination of, 582–84
  evolution of, in animals, 604–5
    in plants, 604
  in animals, 601–63
Sex-chromosomes, 582
Sex hormones, 347, 481–2, 487–8
Sex-linkage, 583–4
Shell, 526
Shell-glands, of *Fasciola*, 41
  of *Taenia*, 48
Shell-membranes, 526
Sieve plates, 231, 338F–9
Sieve tubes, 231, 402
  structure of, 338F–9
Sino-auricular node, 161
Sinus, anterior cardinal, 96, 522, 538
  of *Periplaneta*, 73
  posterior cardinal, 96, 522, 538
  venosus, 93F, 123, 126, 129, 161, 538, **608**, 609, 611
Sinusoids, of liver, 341–2F
Skeletogenous layer, 86
Skeleton, of *Oryctolagus*, 141–51
  of *Rana*, 112F, 113–21
  of *Scyliorhinus*, 84–9
Skin, of *Oryctolagus*, 140F–1
  of *Rana*, 111F–12
  of *Scyliorhinus*, 83F
Skull, of dog, 147F, 148F, 149F, 150–4
  of *Oryctolagus*, 147F–8
  of *Rana*, 113F, 114F
  of *Scyliorhinus*, 85F, 87–90
'Sleep', of flowers and leaves, 476
Sleeping-sickness, 21
Smell, mammalian organs of, 173
Sodium bicarbonate, 327, 356, 391
Soft commissure, 163
Soil, 645–50
Sol, 5, 305, 307
Solar plexus, 166, 467
Soma, 353
  evolution of in plants, 353, 605
Somatopleur, 505
Sorus, 224F, 225–6
Spathe, 258
Species, 626
Specific adhesion, 516–17, 562
Speech, significance of, 473
Spermaphyta, 219, 238, 642
Spermatheca, of *Lumbricus*, 53, 62
  of *Periplaneta*, 78
Spermatic cord, 174
Spermatids, 319
Spermatocytes, 319
Spermatogenesis, 318–19F, 482
Spermatogonia, 318
Spermatophores, 106
Spermatozoa, maturation of, 319
  of *Hydra*, 32
  of vertebrates, 347F–8
Spermatozoids, of *Dryopteris*, 228
  of *Fucus*, 196
  of *Pellia*, 217, 218
Spermatozoön, structure of, 319, 348F–9
Sperm-sac, 107
Sphincter muscle, 90, 121
Spike, 273F
Spinal cord, 99–100, 131, 164, **461**, **470**
Spinal nerves, 101, 103, 132–3F, 165
Spine, modified leaf, 255

modified stem, 239F
Spiracle, of *Periplaneta*, 75
of *Scyliorhinus*, 82, 90, 91
Spirillum, 211
Spirogyra, 187–9, 305, 352
Splanchnocoel, 173, 505, 531
Splanchnocranium, 87, 115, 151
Splanchnopleur, 505
Spleen, 90, 126
Spongy parenchyma, 260
Sporangiophore, 204–5
Sporangium, of *Dryopteris*, 225
of *Mucor*, 204
Spore, 212, 218, 223, 226, **556–8**
of *Mucor*, 204
Sporoblast, of *Monocystis*, 15
of *Plasmodium*, 19
Sporocyst, of *Fasciola*, 42, 43F, 44
of *Monocystis*, 15
Sporogonium, of *Funaria*, 221–2F
of *Pellia*, 218–19F
Sporont, of *Monocystis*, 15
of *Plasmodium*, 19
Sporophyte generation, 216, 219, 225, 228, 237, **557**, 600
development of in *Dryopteris*, 228–9
Sporozoites, of *Monocystis*, 15–16
of *Plasmodium*, 19
Sporulation, in *Amoeba*, 6, 8
Stadia, 80
Stamen, 264, **268**, **275**
Staminate cones, 233F, 234
Staminodes, 598
Standard (petal), 271
Staphylococci, 211
Starch, 370
digestion of, 391
grains, 182, 404F, 405
presence of in green leaf, 415
transitory, 405, 406
Statocyst, 36, 37F
Statolith, 36
Stearin, 372
Stele, 243
Stellate cells, 344, 473
Stem, external form of, 238
herbaceous, shrubby and woody, 238
internal structure, 242–51
of Dictotyledon, 242, 243F, 244F
of Monocotyledon, 250F–1
of *Dryopteris*, 225
of *Pinus*, 231F
practical work, 251–2
Sterigmata, 216
Sterilisation, 212–13
Sternebrae, 143
Sternum, of *Oryctolagus*, 143
of *Periplaneta*, 71
Stigma, of *Chlamydomonas*, 182
of *Euglena*, 643
of carpel, 238, 268–9
Stigmata, of *Periplaneta*, 75
Stipe, of *Fucus*, 192, 194
Stipules, 255
Stolon, 240
Stoma, 225, 233, 243, **260–1**
mechanism of, 404F–5
Stomach, of medusa, 36
of *Oryctolagus*, 155–6
of *Rana*, 121
of *Scyliorhinus*, 90
structure of wall of, 341
Stomium, 226
Stomodaeum, 72, 79, 332
Storage, 343–4, 406–8
in animals, 343–4, 406
in plants, 240, 256, 406–8
Stratum corneum, 83, 113, 140, 333
Stratum granulosum, 140
Stratum lucidum, 140
Stratum Malpighi, 83, 113, 140, 141, 332
Streptococci, 211
Strobila, 45
Strobilisation, 48, 560
Stroma, 395
'Struggle for existence', 617, 624
Style, of carpel, 268–9
of *Periplaneta*, 71
Sub-cephalic pocket, 529–30
Suberin, 251, 305
Sub-intestinal blood-vessel, 522, **607**, 611
Sub-oesophageal ganglion, of *Periplaneta*, 76
Succus entericus, 391
Sucker, of *Taenia*, 45
as propagatory shoot, 240
Sucrase, 391
Sucrose, 370, 393
Suction pressure, 378
Sulphur (circulation of), 412–14
Superior (gynaecium), 266
Superlingua, 71
Supination, 145
Supra-dorsal cartilages, 86
Supra-oesophageal ganglia, of *Periplaneta*, 76, 77
Supra-pharyngeal ganglia, of *Lumbricus*, 60–1, 66

Supra-renal body, 109, 138
Survival, of seed plants, 285
'Survival of the fittest', 617
Suspensor, of Angiospermae, 280–1F
of *Pinus*, 236
Suspensory ligament, 167, 169
Sutures, 149
Swarming, 363–4
Sweat glands, 141
Sweet pea, 271–2F
Sylvian fissure, 162
Symbiosis, 392, 411, 669–71
Sympathetic nervous system, *see* Autonomic nervous system
Sympathetin, 468
Sympetalous, 268
Symphysis, 116, 117, 145
Symplast, 384
Sympodium, 239, 242F
Synapse, 462, 463
Syncarpous, 268
Synergidae, 277
Syngamy, 556–7, 604

TADPOLE, development of, 523–5
Taenia coenurus, 51
echinococcus, 51, 560
metotica, 51
sagginata, 51
serrata, 51
solium, 44–51
Tail, 48–9
Tapetum, of Angiospermae, 275
of *Dryopteris*, 226
of eye of *Scyliorhinus*, 170
Tapeworm, *see Taenia solium*
respiration in, 438
Tannins, 449, 451
Tarsals, 119, 146
Tarsus, of *Oryctolagus*, 145F
of *Periplaneta*, 71
of *Rana*, 110, 119
Taste buds, 172F–3
Taxes, 454–5
Tectorial membrane, 172
Teeth, of *Oryctolagus*, 151–6
development of, 152F, 153
structure of, 151, 152, 153
of *Rana*, 120–1
of *Scyliorhinus*, 83
vomerine, 114, 121
Teicholic acids, 211
Telencephalon, 98, 130, 131, 162
Temperature, effect of, on germination, 553
on growth, 420
regulation of, 622
Tendon, 323
Tendril, as modified leaf, 255
as modified stem, 239
Tentacles, 25, 27
Tergum, 71
Terminal arborisation, 336
Termites, 363–4
Terpenes, 450
Testa, of Angiosperm seed, 280
of *Pinus* seed, 236
Testes, of *Fasciola*, 41
of *Hydra*, 25, 32
of *Lumbricus*, 62–3
of mammals, 347F–8, 487
of *Obelia*, 37
of *Oryctolagus*, 174
of *Periplaneta*, 78
of *Rana*, 135
of *Scyliorhinus*, 106
of *Taenia*, 47–8
Thallus, of *Fucus*, 192
of *Pellia*, 216
Therapsida, condition of heart in, 608
Thickening, of walls of vessels, 337F
Thoracic duct, 162
Thorax, of *Oryctolagus*, 156
of *Periplaneta*, 71
Thrombase, 356
Thrombokinase, 356
Thumb-pad, 110, 131
Thymus, development of in *Rana*, 521
homology of, 521, 598
hormone of, 486
of *Oryctolagus*, 176
of *Rana*, 138
of *Scyliorhinus*, 109
Thyroid cartilage, 151, 156
Thyroid gland, development of in *Rana*, 519–21
homology of, 506, 598
of *Oryctolagus*, 176
of *Rana*, 138
of *Scyliorhinus*, 109
structure of, 345–6F
Thyroxin, 345, 480–81
Tibia, of *Periplaneta*, 71
Tidal volume, 424
Tissues, 321 *et seq.*
conducting, of plants, 337, 338F, 339
mechanical, 321–8
muscular, 333, 334F, 335
nervous, 335, 336F, 337
practical work, 349–50
surface, 328–9

Tongue, of *Oryctolagus*, 155
of *Rana*, 120
Tongue-bars, 506, 521
homology of, 598
Tonsils, 157
Toothwort, *see Lathroea*
Toxins, 212
Trabeculae, of bone, 549
of ear, 105
Trace elements, 376
Trachea, of *Oryctolagus*, 156
of *Periplaneta*, **71**, 75, 79, 426
Tracheids, 231
structure of, 338F–9
Tracheoles, 75
Transfusion tissue, 233
Translocation, 402–4
Transpiration, 380–2
conditions affecting, 380–1
measurement of, 387–8
rate of in xerophytes, 652–3
Transpiration current, 380–1
Transverse process, 87, 116, 142–3
Trichocyst, 9
Trichonympha, 364
Triploblastica, 65, 81
Triton cristatus and *taeniatus*, experiments on development of, 513–15
Trochlea, 117, 144
Trophoblast, 540
Trophozoites, 14, 16
Tropisms, 455–9
Truncus arteriosus, 123, 125, 608
Trypanosomes, 21–3, 24
Trypsin, 391
Trypsinogen, 391
Tube nucleus, 279
Tuber, 241F
Tuberculum, 141, 143
Tubularia, 559–60
Tulip, 273
Tunica, 246
Turgor pressure, 189, 378–9
Tylose, 261
Tympanum, 110, 115, 135, 172
Typhlosole, 55, 57, 393

UMBEL, 273F
Umbelliferae, 266
Umbilical cord, 176, 543, 563
Undulating membrane, of Trypanosomes, 21
Ungulata, 475F
Unusual nutrition, 656 *et seq.*
Urea, 135, 327, 447
Ureter, 174, 445, 539, **614**, **615**
Urethra, 175
Uric acid, 445
Urinary bladder, 121, 135, 174, 175
papilla, 108
Urino-genital papilla, 107
sinus, 107
system, evolutionary development of, 613–15
of *Oryctolagus*, 174–6
of *Rana*, 135–7
of *Scyliorhinus*, 105–8
Uterus, of *Fasciola*, 41
of *Oryctolagus*, 175, 543
of *Taenia*, 48
Utriculus, 104, 134

VACUOLE, 17, 182, 187
contractile, 4–7, 8, 9, 11, 14, 182, 187, **442**, 643
food, 4, 6, 11
formative, 9
Vagina, of *Oryctolagus*, 175
of *Taenia*, 48
Valve, 93, 123
mitral, 158
semi-lunar, 93, 123, 158
spiral, of *Rana*, 123, 608
of *Scyliorhinus*, 90, 93, 393
tricuspid, 158
Variation, 617–19
continuous, 618
genotypic, 618–19
meristic and substantive, 618
origin of, 618, 624–5
phenotypic, 616, 618–19
physiological, 618
Vas deferens, of *Lumbricus*, 53, 63
of *Scyliorhinus*, 106
origin of, 614, 615
Vasa efferentia, of *Rana*, 135
of *Scyliorhinus*, 106
origin of, 614, 615
Vascular bundles, 243–4, 268
of leaf, 260
of root, 291F–2F
of stem, of Dicotyledons, 243–5
of Monocottledons, 250F–1
Vascular system, development of, in *Rana*, 522–23
in *Gallus*, 536–8
evolution of in Vertebrata, 607–13F
of *Lumbricus*, 56–8
of *Oryctolagus*, 157–8
of *Periplaneta*, 73–5
of *Rana*, 121–30

of *Scyliorhinus*, 93–7
Vasopressin, 484
Vaucheria, 189–90
Vegetative cell, 235
Vein, 121, 340, 610–12
see also Venous system
Vein, of leaf, 260
Velamen, 666
Velum, of *Branchiostoma*, 506
of medusa, 35
Venation, 254
Venous system, evolutionary development of, 611, 612F, 613
of *Oryctolagus*, 161–2
of *Rana*, 127–9
of *Scyliorhinus*, 95F, 96–7
Venter, 217, 221, 227
Ventilation movements, of *Scyliorhinus*, 91
Ventral aorta, 608
development of in *Rana*, 521–22
of *Scyliorhinus*, 92F, 93, 608
Ventral root, of nerve, 103, 133, 462F
Ventricle, of brain, 99, 131, 164
of heart, 93, 123, 131, 157, 163, 164, 608
Vermis, 163
Vernalin, 554
Vertebrae, of *Oryctolagus*, 141–3
of *Rana*, 116
Vertebral column, of *Oryctolagus*, 141, 142F, 143
of *Rana*, 112F
of *Scyliorhinus*, 84–5F
Vertebral plate, 517
Vertebrarterial canal, 142
Vertebrata, 618–20, 626
Vesicula seminalis, of *Fasciola*, 41
of *Lumbricus*, 62F, 63
of *Oryctolagus*, 174–5
of *Periplaneta*, 78
of *Rana*, 135
of *Scyliorhinus*, 107
Vessels, of xylem, 231
structure of, 337F–9
Vestibule, 176
Vestigial organs, 598
Vibrissae, 140
Villus, 156, 340–1F, 355, 393F–4
Violaceae, 633F–4
Visceral arch, 87, 90
Viruses, 214
Vision, physiology of, 169–70
Visual purple, 169
Vital dye staining, 510, 529
Vitamins, 343, 372, 375, 376
Vitelline cell, of *Taenia*, 48
Vitelline membrane, 526
Vitrellae, 78
Vitreous humour, 167
Viviparous, 176, 561
Vocal cords, 156
Vocal sacs, 121
Volvents, 27–8
Volvox, 185–7
differentiation of sex in, 186, 353
individuality in, 364, 365
Vomer, 114, 147
Vulva, 139, 175

WALLFLOWER, 270, 631F
Waste matter, 441
elimination of, 355, 441–52
in animals and plants compared, 451, 642
Water, as animal food, 373–5
importance of, in development of *Gallus*, 526–7
in germination, 553
raising of up stem, 381–2
Water-cultures, 386–7F
Water-pore, 381–2
Water-supply, of plants, 650–53
Wheel-organ, homology, 598
White ants, 363–4
White matter, 99, 131, 463–4
Wings, of bats, 476
of birds, 475
of insects, 474
of *Periplaneta*, 71
of Pterodactyls, 622
of sweet pea, 271
Wolffian duct, condition of in Gnathostomata, 613–14
development of, in *Gallus*, 539
in *Rana*, 518F, 519
of *Oryctolagus*, 174
of *Rana*, 518F, 519
of *Scyliorhinus*, 105–7, 108
origin of, 614–15
Wood, *see* Secondary xylem
Writing, significance of to man, 473

X-CHROMOSOME, 582, 583
Xanthophyll, 395
Xerophytes, 256, 652–3
Xiphoid cartilage, 117, 143
Xylem, of leaf, 233, 260
of root, 225, 291, 296F
of stem, 244
primary, 231, 249, 296F
secondary, 231, 249, 296F

structure of, 337F, 338F, 339

Y-CHROMOSOME, 582, 584
Yeast, 207–8, 435
Yolk, 41, 48, 508, 535, 536
Yolk-glands, of *Fasciola*, 41
of *Taenia*, 48

ZOOCHLORELLAE, 28, 669
Zoogloea, 211
Zoosporangium, of *Pythium*, 201
Zoospore, of *Pythium*, 201–2
Zooxanthellae, 28, 669
Zygapophyses, 116, 142
Zygomatic arch, 151
Zygomorphic, 267, 286
Zygospore, of *Chlamydomonas*, 183F–4
of *Mucor*, 205
of *Spirogyra*, 188, 563
Zygote, 183–4, 187, 202, **556–7**
Zymase, 435